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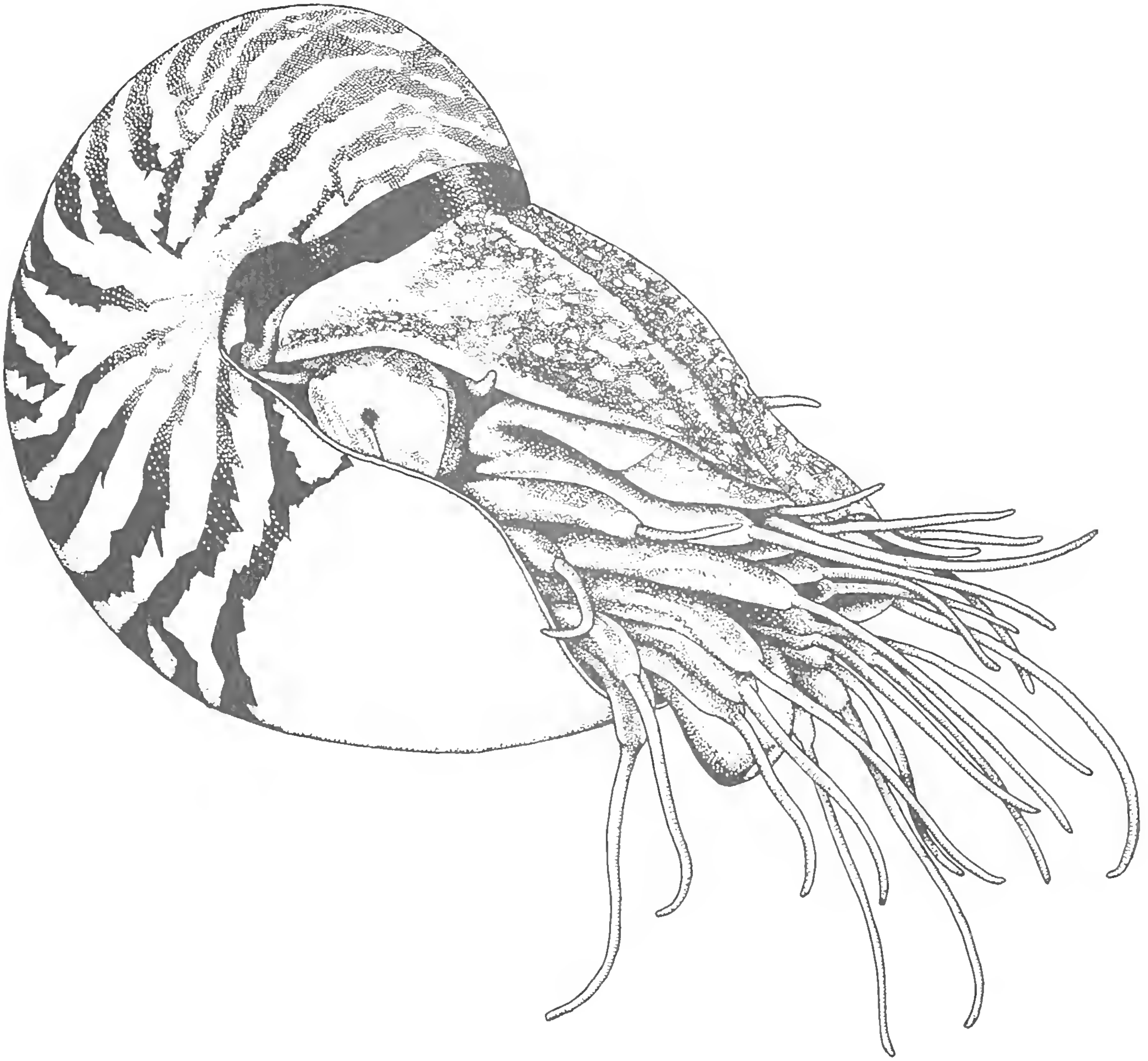

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CONTENTS

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FLORIDA Arts

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Ecological separation of the mudwhelks *Terebralia sulcata* (Born, 1778) and *T. semistriata* (Mörch, 1852) (Gastropoda: Potamididae) from northern Australia

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ABSTRACT

Until recently, two species were recognized in the potamidid genus *Terebralia*: *T. palustris* (Linnaeus, 1767) and *T. sulcata* (Born, 1778). Houbrick (1991) separated *T. semistriata* (Mörch, 1852) from *T. sulcata*, based on a detailed examination of shells, radulae, anatomy, and geographical distributions. The present paper provides comparative data on geographical distribution along the Australian coast, habitat, size frequency characteristics, and densities of the two species, which provides further confirmation that separate specific status is warranted.

Additional key words: Cerithioidea, mangroves, taxonomy, ecology

INTRODUCTION

The Potamididae is one of the dominant families of mollusks in mangroves in the Indo-West Pacific region. In particular, mudwhelks of the genera *Terebralia* and *Telescopium* are among the largest and most visible of mangrove mollusks, and are key components of the ecosystem (McNae, 1967; 1968; Plaziat, 1977; 1984; Wells and Lalli, in press). In a series of studies in the Bay of Rest, northwestern Australia, and in Hong Kong, Wells (1980, 1983, 1984a, 1984b, 1986, 1990) demonstrated the importance of *Terebralia* (the Bay of Rest population was identified in the papers as *T. sulcata* but is now considered to be *T. semistriata*). For example, *Terebralia semistriata* comprised 55% of the biomass of all invertebrates in the *Avicennia* zone of the mangroves in the Bay of Rest. Both *T. palustris* and *T. semistriata* can attain significant densities (often above $100\ m^{-2}$) within mangroves, but populations reach to the edge of the *Avicennia* pneumatophores and no further (Wells, 1986).

In recent years there has been an increase in studies of *Terebralia*, including their general biology (Soemodihardjo and Kastoro, 1977; Rambabu et al., 1987), feeding (Nishihira, 1983; Slim et al., 1997), early growth (Rao, 1938; Hashimoto and Nishijima, 1987), historical declines in populations (Ohgaki and Kurozumi, 2000), comparative ecology (Wells, 1980), and relationship to canopy cover (Crowe, 1997; Crowe and McMahon (1997).

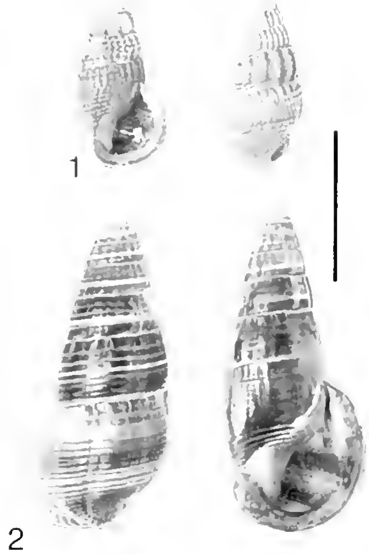
Until 1991, all ecological studies recognized only two species of *Terebralia*: *T. palustris* (Linnaeus, 1767) and *T. sulcata* (Born, 1778). In a major revision of the group, Houbrick (1991) recognized a third species of *Terebralia*, separating *T. semistriata* (Mörch, 1852), a taxon previously considered to be a synonym of *T. sulcata*. The work was based on a wide combination of characters, including shells, radulae, anatomy, and geographical distributions. Wilson (1993) considered the division of *T. sulcata* into two closely related species required confirmation based on ecological separation of the species. The present paper compares the ecology of *T. semistriata* and *T. sulcata*, confirming that separate specific status is warranted.

MATERIALS AND METHODS

Terebralia semistriata and *T. sulcata* were found to occur in separate portions of the same mangrove systems during a collecting expedition made to Darwin Harbour, Northern Territory, in June 1986. The two species were tagged for growth studies at Mandorah (12°51′ S; 130°32′ E) in May and December 1999 respectively and were monitored at approximately six monthly intervals. The comparative study of the two species reported here was made from 21 to 26 May 2001, on the last visit for the growth studies.

The two species were readily identified in the field using shell characters described by Houbrick (1991). The shell of *Terebralia semistriata* is larger and heavier than *T. sulcata*, has weaker sutures, is weakly sculptured with flattened spiral cords, and lacks axial ribs.

A 30 m transect tape was placed perpendicular to the shoreline at the front of the mangroves (*Terebralia sulcata*) and at the back of the mangroves (*T. semistriata*). A $1\ m^2$ quadrat was searched every 2 m from the seaward or landward fringe of the mangroves until the limit



Figures 1, 2. Shell of *Terebralia sulcata* (1) and *T. semistriata* (2) from the mangroves at Mandorah, Darwin Harbour, Northern Territory. Scale bar = 30 mm.

of the snail populations. All snails encountered were counted and measured to the nearest 1 mm with calipers. Four transects were made at 5 m intervals along the shoreline for *T. sulcata* and at 3 m intervals for *T. semistriata*.

The habitats occupied by the snails were also noted when searching the transects. Additional snails were collected in the area to obtain 500 measurements for *Terebralia semistriata* and as many as possible for *T. sulcata*, as there were insufficient *T. sulcata* in the area to measure 500 individuals. Total shell length was measured to the nearest 1 mm with calipers. An inflated outer lip is formed when the animals mature, after which no further increase in shell length occurs (Houbrick, 1991). Positions of *T. sulcata* on mangroves or sediment surface were measured to the east and west of a small tidal creek. Fifty animals were counted in each habitat. To be considered to be on the mangrove, the snail had to have the shell apex off the ground; animals lying on the mud surface with their foot attached to a mangrove were considered to be on the sediment.

Shore heights of the populations were determined on the afternoon of 22 May 2001. The time when the lower portion of the *Terebralia sulcata* population became covered on the rising tide was noted, and the tide followed up the shoreline. Shore heights were determined by comparison with the Australian National Tide Tables (Department of Defence, 2000) for Darwin Harbour. Tides in the harbour are predominantly semidiurnal with a maximum range during the year of 7.8 m. The mean neap tidal range is 1.9 m, while springs average 5.5 m.

Data on geographic distributions of the two species were obtained by examining specimens in the Australian Museum, Sydney (AMS), The Natural History Museum, London (BMNH), National Museum of Natural History, Smithsonian Institution (USNM), Western Australian Museum (WAM) and the Zoological Museum, Copenhagen (ZMC).

RESULTS

Populations of the two species (Figures 1, 2) were clearly separated in the mangroves at Mandorah. *Terebralia sulcata* occupies the seaward zone of the mangroves at a mid-tidal level of 1.9 to 5.3 m (Table 1). The site is near a channel behind an intertidal sand beach, and is occupied by a mixed mangrove assemblage, including two large *Avicennia marina* trees, one of which is approximately 6 m high, small (< 2 m) *Ceriops australis*, and isolated trees of *Rhizophora stylosa*. The mangroves vary in size from small saplings a few centimeters high to full grown *R. stylosa*. The channel bank slopes steeply up to the mangrove zone, where the shore levels off. The muddy sand is then relatively flat, with shore height increasing by 0.4 m over a horizontal distance of about 25 m. This flat area is occupied by *T. sulcata*. Shoreward

Table 1. Comparison of the mudwhelks *Terebralia sulcata* and *T. semistriata* in the mangroves at Mandorah, Darwin Harbour, Northern Territory. The difference between habitats occupied to the east and west of the tidal creek was statistically significant (χ^2 = 19.6, $p < 0.05$).

Characteristic	*Terebralia sulcata*	*Terebralia semistriata*
Position in mangroves	Seaward margin	Shoreward margin
Shore height	1.9–5.3 m	6.4–6.6 m
Habitat	On sediment surface; also climbs mangrove trees, shrubs and pneumatophores to a height of up to 60 cm	On sediment surface; never climbs up mangroves
Density	Mean 0.4 ± 0.4 m^{-2}	Mean 1.3 ± 0.3 m^{-2}
Size (to nearest 1 mm)	Small. Mean length of population 28.5 ± 0.7 mm (n = 196), range 13–44 mm. Adults: Mean length 33.7 ± 0.4 mm (n = 82), range 26–43 mm	Large. Mean length of population 40.5 ± 0.8 mm (n = 498), range 13–69 mm. Adults: Mean length 60.6 ± 0.3 mm (n = 113), range 51–69 mm.
Other potamidids present	None	*Terebralia palustris, Telescopium telescopium, Cerithidea largillierti*

Table 2. Comparison of *Terebralia sulcata* on the mud surface and on mangroves to the east and west of the small tidal creek at Mandorah, Darwin Harbour, Northern Territory.

Habitat	East of tidal creek	Number of snails west of tidal creek	Total
On sand surface	11	33	44
On mangroves	39	17	56
Total	50	50	100

the mangrove becomes a monospecific forest of large *R. stylosa*.

Terebralia sulcata occur both on the sediment surface and on the lower trunks and leaves of the mangroves to a height of 60 cm, though most occur at less than 30 cm from the surface of the mud. A difference was found between locations of *T. sulcata* on mangroves to the east and west of a shallow tidal creek. The creek is approximately 20 m wide at high tide, but only 5 m at low tide. The eastern side, where the bank is steep, contains a small, monospecific stand of *Ceriops australis*. Seventy-eight percent of the *T. sulcata* were on the trees when surveyed at low tide (Table 2). The animals secrete mucus, which binds them to the mangrove. If the underlying surface is flat, the mucus can form a complete seal and function as an epiphragm. More commonly, the mucus acts to attach only the inner part of the shell aperture to the mangrove. Both adults and juveniles are found on the mud surface and on the mangroves; however there is a tendency for juveniles to predominate on the mangroves and adults on the mud surface.

To the west of the small tidal creek, where the transects were made, *Terebralia sulcata* were most common on the mud surface, with 66% occurring on the mud. The difference between habitats occupied to the east and west of the tidal creek was statistically significant. While no quantitative measurements were made, *T. sulcata* under *Avicennia marina* were largely on the sediment surface, while those in *Rhizophora stylosa* or *Ceriops australis* tended to be on the mangroves.

In contrast to *Terebralia sulcata*, the population of *T. semistriata* occurs at the landward fringe of the mangroves, approximately 100 m to the northwest. The habitat is a sand surface with a mixture of mangrove species, including predominantly *Rhizophora stylosa* and *Avicennia marina*, at a tidal height of 6.1 to 6.6 m. An upper intertidal sand beach commences at a shore height of 6.6 m, forming the upper limit of the population of *T. semistriata*. While some individuals of *T. semistriata* occur amongst the *R. stylosa*, most are on the open mud surface among the *A. marina* pneumatophores. The locations of the snails change somewhat over a two-week tidal cycle as they seek protection from desiccation among the mangrove roots during the neap tides. However, they never climb the mangroves as occurs in *T. sulcata*. Exposed flat rocks in the centre of the mangroves limit the seaward extent of the *T. semistriata* population.

Separation of the two living populations is complete. A total of 744 *Terebralia sulcata* were measured during the tagging experiments; no living individuals of *T. semistriata* were found in the *T. sulcata* population. A total of 2270 *T. semistriata* were measured; only a single living *T. sulcata* was found in the *T. semistriata* population.

There are also differences in the densities of the two populations of *Terebralia*. *Terebralia sulcata* has a very low density of only 0.4 ± 0.1 m^{-2} and did not co-occur with other potamidid species. The mean density of *T. semistriata* was 1.3 ± 0.3 m^{-2}. Three other potamidids occurred in the transects with *T. semistriata*. *Terebralia palustris* and *Telescopium telescopium* (Linnaeus, 1758) had mean densities of 6.1 ± 1.2 m^{-2} and 1.6 ± 0.6 m^{-2} respectively. A single specimen of *Cerithidea largellierti* (Philippi, 1849) was also found.

There is a clear difference in the size frequency characteristics of *Terebralia sulcata* and *T. semistriata* at Mandorah (Table 1; Figure 3). The mean size of adult *T. sulcata* is 33.7 ± 0.4 mm, with a maximum size of 43 mm. In contrast, the mean size of adult *T. semistriata* is 60.6 ± 0.3 mm, with a maximum of 69 mm. Thus the smallest adult *T. semistriata* was 8 mm larger than the largest adult *T. sulcata*.

Examination of specimens in museums shows that the Australian distributional data provided for *Terebralia sulcata* by Houbrick (1991) are inaccurate. Essentially Houbrick assumed the two species had the same geographical range on the north coast of Australia: from Shark Bay, Western Australia, to southern Queensland. *Terebralia semistriata* is in fact widely distributed along the north coast of the continent from Shark Bay, Western Australia, to Keppel Bay on the east coast of Queensland (Figure 4). *Terebralia sulcata* also extends south to Keppel Bay, Queensland, but it is restricted to the Kimberley, from Broome northward, in Western Australia. In the text of his paper, Houbrick (1991) refers to specimens of *T. sulcata* from more southerly localities in Western Australia: Rowley Shoals (USNM 847084) and Bay of Rest, North West Cape (USNM 801606). Specimens of both lots were re-examined for the present paper. The label for USNM 847084 clearly states the specimens of *T. sulcata* were collected in Broome by the Rowley Shoals Expedition. Limited collecting was done in Broome before sailing for the Rowley Shoals. The shoals are open ocean coral reef atolls and no *Terebralia* occur there (Wells and Slack-Smith, 1986). The specimen from the Bay of Rest (USNM 801606) was apparently first considered to be *T. sulcata* by Houbrick. He later changed his mind and included the specimen in *T. semistriata* in the Smithsonian collection, but apparently neglected to change his written notes. That specimen and all others collected in the Bay of Rest are in fact *T. semistriata*.

DISCUSSION

The present paper demonstrates *Terebralia semistriata* and *T. sulcata* are clearly separated ecologically. There

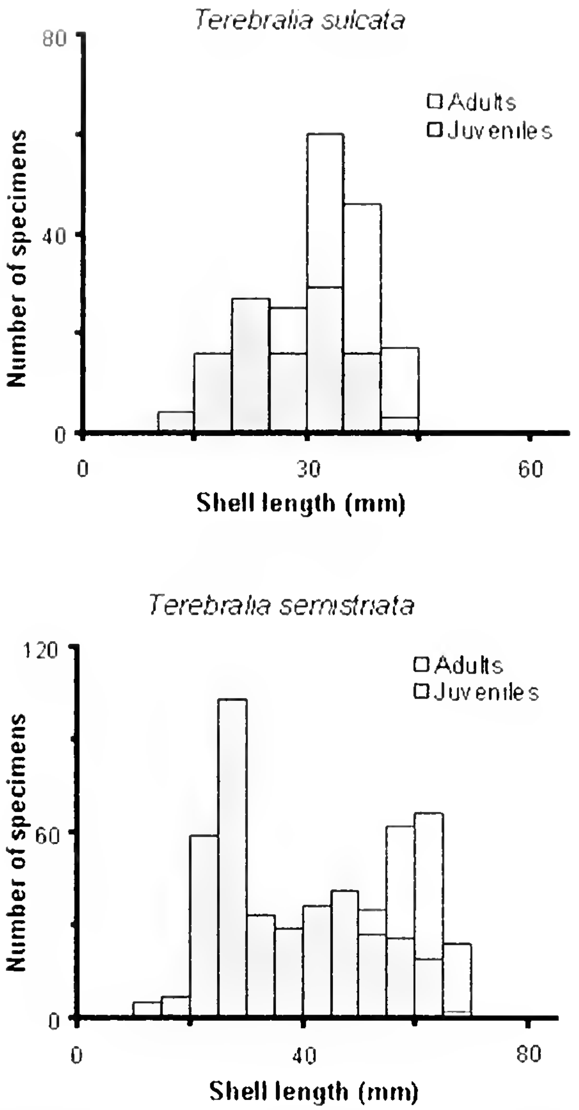


Figure 3. Size frequency histograms of *Terebralia sulcata* (upper) and *T. semistriata* (lower) collected in the mangroves at Mandorah, Darwin Harbour, Northern Territory from 21 to 26 May 2001.

are substantial differences in their geographical distributions. Houbrick (1991) examined numerous specimens of *T. sulcata* from a wide range in the western Pacific Ocean, including Malaysia, Vietnam, Indonesia, Papua New Guinea, Philippines, China, Ryukyu Islands, and the Caroline Islands. In contrast *T. semistriata* is limited to the north coast of Australia and southern New Guinea.

In northern Australia, *Terebralia sulcata* is limited to the coast between Broome, Western Australia and Keppel Bay, Queensland. *Terebralia semistriata* occurs in the entire range occupied by *T. sulcata* in northern Australia, but is also common in the large stretch of coast between Shark Bay and Broome, Western Australia. In the region between Broome and Keppel Bay, the two species of *Terebralia* are sympatric in that they inhabit the same mangrove systems, but they occupy separate areas of the mangroves. Where the two species live in the same mangrove, *T. sulcata* lives in the seaward, mid-intertidal portions of the mangroves, while *T. semistriata* lives in the shoreward, upper portions of the mangroves. *Terebralia sulcata* lives both on the mud surface and also climbs up to 60 cm up the mangroves; in contrast, *T. semistriata* are always on the sediment surface and never climb up the mangroves. Shells of *T. semistriata* are significantly larger than those of *T. sulcata* from the same mangroves.

Information on the segregation of the two species at Mandorah was collected incidentally to a major tagging program conducted to study growth in all three species of *Terebralia*. Expeditionary surveys of mollusks in the Kimberley region of Western Australia and near Gove in the Northern Territory (Wells, unpublished) have found a number of mangroves where similar segregation occurs between populations of *T. sulcata* and *T. semistriata*. Because of the considerable expense of working in remote areas, only the Mandorah populations could be examined in detail.

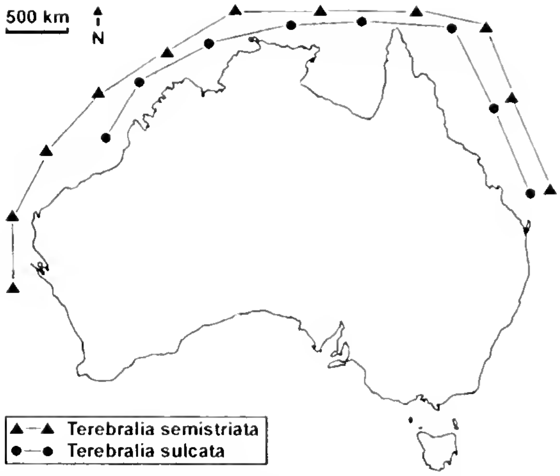


Figure 4. Geographical distribution of *Terebralia sulcata* and *T. semistriata* in northern Australia.

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Dr. J. R. Hanley, then of the Northern Territory Museum, provided detailed knowledge of Darwin Harbour in my early expeditions to the area and extensively discussed *Terebralia* with me. My subsequent research on this genus has benefited greatly from these discussions. I thank the publicans and staff of the Mandorah Beach Hotel for their warm hospitality during my visits to Mandorah. Dr M. G. Harasewych kindly arranged access to the mollusk collections of the Smithsonian Institution; Ms. Kathie Way to those of the BMNH; and Dr. Jorgen Knudsen to the Zoological Museum, Copenhagen. Mr. Ian Loch and Dr. Winston Ponder generously provided distributional information from the Australian Museum, Sydney. Mr. Clay Bryce and Mr. Corey Whisson provid-

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Two new species of *Neolepton* Monterosato, 1875 (Bivalvia: Neoleptonidae) from South Georgia Islands, South Atlantic Ocean

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ABSTRACT

Two new neoleptonid species from South Georgia Islands are described. *Neolepton georgianum* new species is characterized by a medium size shell, smooth shell surface, and ovate shell outline, slightly pointed at anterior end. *Neolepton holmbergi* new species is a small size species, sculptured with well-marked and regularly spaced commarginal ribs. Moreover, the record of *Neolepton powelli* from South Georgia Islands is brought into question.

Additional key words: Systematics, South Atlantic Ocean

INTRODUCTION

Neolepton Monterosato, 1875, is a shallow-water worldwide genus of small Neoleptonidae bivalves. Recently, Salas and Gofas (1998) provided a comprehensive systematic revision of the genus, including a detailed anatomical description of the type species, *Neolepton sulcatulum* (Jeffreys, 1859).

Five *Neolepton* species are known from the Magellanic Region: *Neolepton cobbi* (Cooper and Preston, 1910), *Neolepton bennetti* (Preston, 1912), *Neolepton concentricum* (Preston, 1912), *Neolepton lupei* Soot-Ryen, 1957, and *Neolepton falklandicum* Dell, 1964. None of these species have been reported from South Georgia Islands (Bernard, 1983; Salas and Gofas, 1998; Valdovinos Zarges, 1999).

Dell (1964) described *Neolepton powelli* from Macquarie Island and allocated specimens from South Georgia Islands to that species despite slight differences in shell outline and hinge details between the two localities. In the same paper, Dell (1964) misidentified neoleptonid specimens from Shag Rocks, near South Georgia Islands, as *Neolepton parasiticum* (Dall, 1876), a species belonging in the genus *Waldo* Nicol, 1966 (Nicol, 1966) and excluded from the Neoleptonidae (Salas and Gofas, 1998; Zelaya and Ituarte, 2002).

In the present paper two new neoleptonid species from South Georgia Islands are described.

MATERIALS AND METHODS

The studied material was collected by the R/V EDUARDO L. HOLMBERG, from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) during the April 1996 cruise to South Georgia Islands arranged by the Instituto Antártico Argentino (Figure 1). Samples were taken with a drag net, fixed in 10% buffered formalin and transported to the laboratory where bivalves were sorted from sediments using a stereoscopic microscope and preserved in ethanol.

The studied species were fully described and illustrated using scanning electron microscope (SEM) pho-

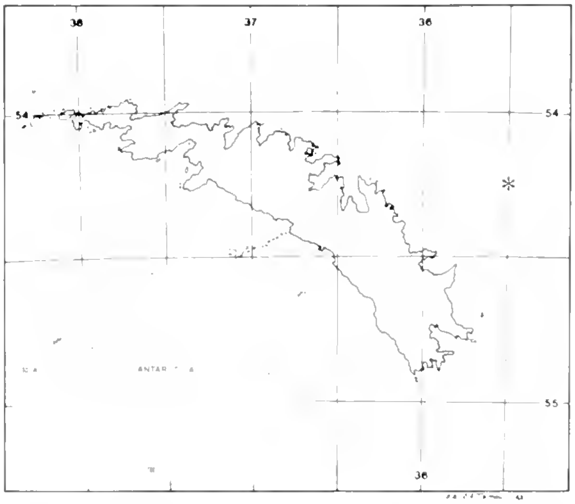
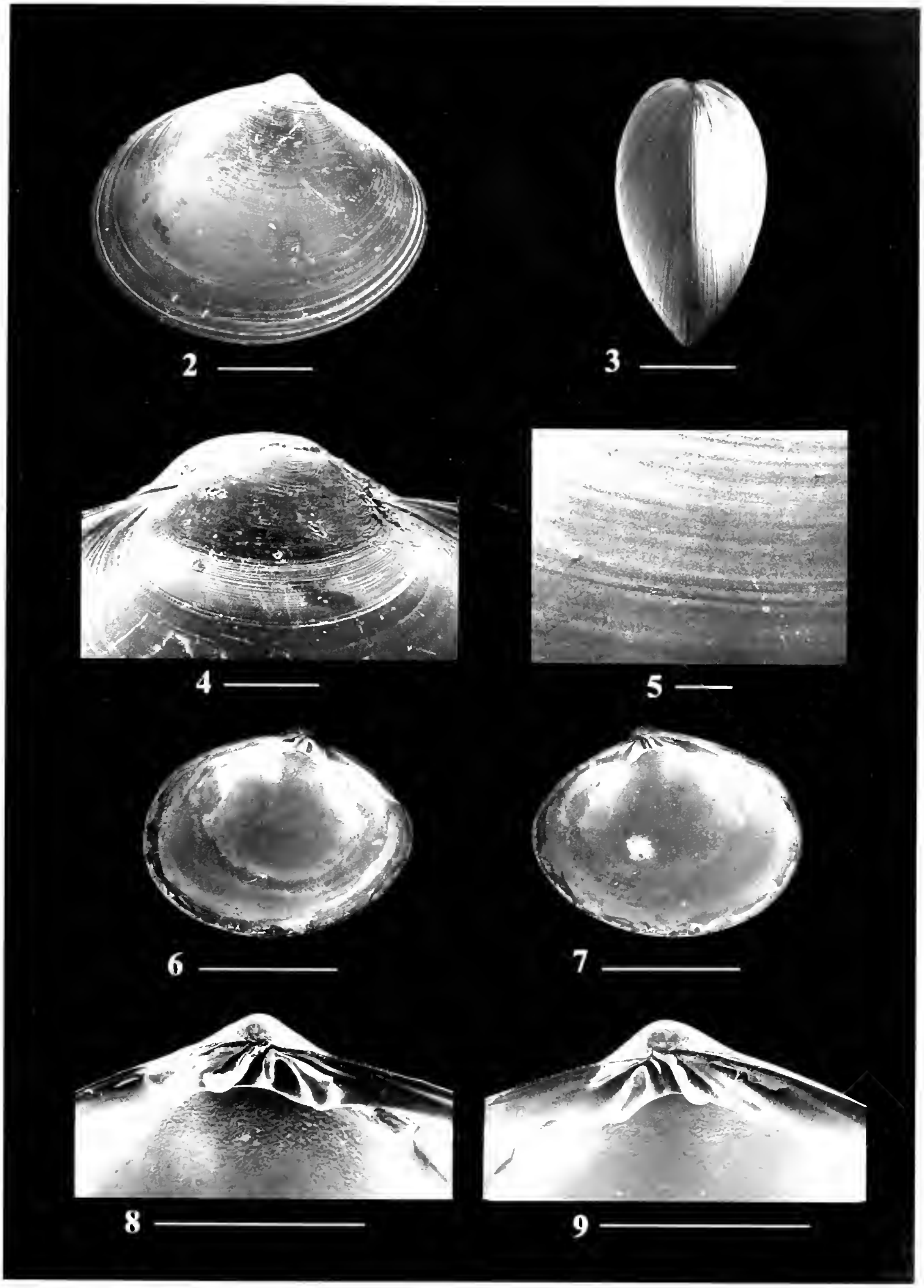


Figure 1. Location map showing the type locality (*) for *Neolepton georgianum* new species and *N. holmbergi* new species.



Figures 2–9. *Neolepton georgianum* new species. **2.** Holotype MLP 6733-1, lateral view of the right valve. **3–9.** Paratypes MLP 6733-2. **3.** Posterior view. **4.** Detail of the protoconch. **5.** Shell surface sculpture. **6.** Inner view of a left valve. **7.** Inner view of a right valve. **8.** Left valve, detail of hinge. **9.** Right valve, detail of hinge. Scale bars: Figures 2, 3, 6–9 = 1 mm; Figures 4, 5 = 100 µm.

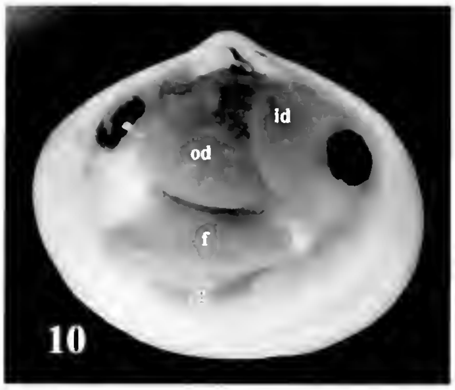


Figure 10. *Neolepton georgianum* new species. A partially dissected specimen (L = 3.3 mm) showing details of soft parts anatomy. **f:** foot; **g:** gland cells of the mantle edge; **id:** inner demibranch; **od:** outer demibranch.

tography. Hinge teeth terminology follows Bernard (1895, 1898) and Salas and Gofas (1998). Shell measurements were recorded according to the following criteria: shell length (L): maximum anteroposterior distance; shell height (H): maximum dorsoventral distance, perpendicular to length; shell width (W): maximum distance across valves. Morphometric ratios H/L and W/H were calculated. In the text, number of specimens measured (n), mean, and standard deviation are given. Voucher specimens were deposited in Museo de La Plata, La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN) and Muséum National d' Histoire Naturelle, Paris (MNHN).

For comparative purposes, types of *Neolepton lupei* from the Swedish Museum of Natural History, Stockholm (SMNH), and photographs of the holotype of *N. powelli* from the Natural History Museum, London (NHM) were used.

SYSTEMATICS

Neolepton georgianum new species
Figures 2–10

Description: Shell delicate, medium sized (maximum L = 3.4 mm), not inflated (ratio W/H = 0.51 ± 0.03, n = 12), shell outline ovate, somewhat elongate, high (ratio H/L = 0.83 ± 0.02, n = 12), somewhat inequilateral, posterior end larger and wider than anterior one, which is slightly pointed; anterior and posterior half of dorsal margin only slightly curved, ventral margin evenly and widely arcuate; anterior margin short, acute, posterior margin widely and evenly curved. Beaks very small, sharply triangular slightly displaced forward, clearly outstanding from shell surface and well visible above dorsal margin. Protoconch well-marked, smooth, not much inflated, about 300 μm long. Shell surface brilliant, periostracum pinkish, faintly sculptured with very low, irregularly spaced, commarginal ribs.

Hinge plate strong, narrowing moderately below the beaks. Left valve: cardinal 2a relatively short, straight, greatly enlarged at posterior half; cardinal 2b relatively long, forming a hook with 2a, posterior lateral PII short, strong and well outstanding from dorsal margin. Right valve: cardinal 1 high, with distal cusp and short base nearly perpendicular to anteroposterior axis; 3a slender and low, 3b quite short and very thin. PI well developed, elongate, with distal cusp.

Inner and outer demibranchs present; the outer demibranch, shorter, represents approximately the half of the inner one. Branchial filaments of outer and inner demibranchs sloping toward the anterior end. Inhalant aperture and exhalant siphon bordered by a single row of short tentacles. Large glandular cells of the mantle edge at both sides of the pedal aperture were present and well visible by transparence.

Type Material: Holotype, MLP 6733–1; Paratypes: 20 MLP 6733–2, 10 MACN 35289; 10 MNHN unnumbered; all from the type locality, R/V Eduardo L. Holmberg, 8 April 1996.

Other Material Examined: >60 specimens from the type locality (MLP 6733–3, MACN 35290).

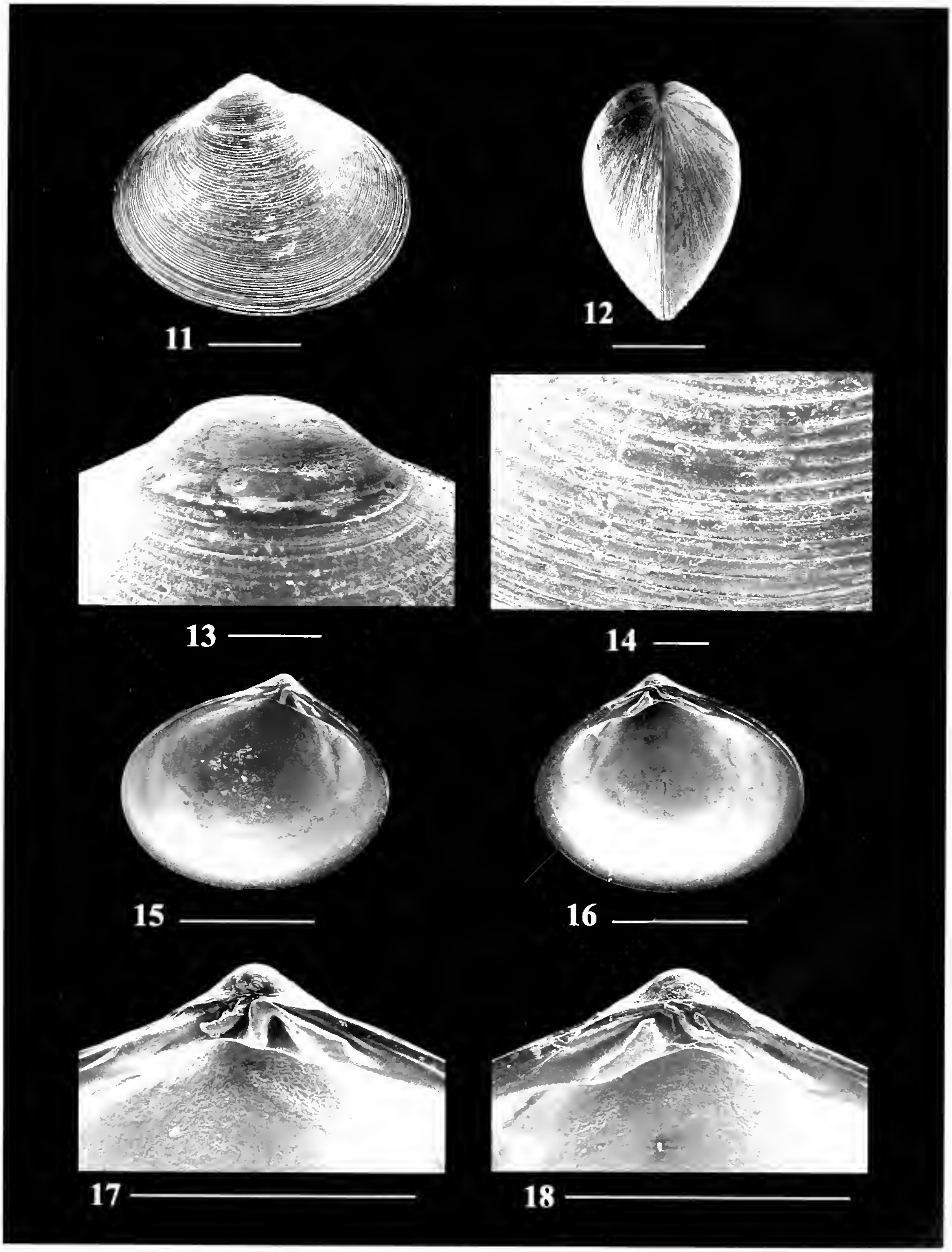
Type Locality: 54°18′ S, 35°30′ W, South Georgia Islands, 94 m.

Distribution: The species is only known from the type locality.

Etymology: The species is named after the South Georgia Islands, the type locality.

Remarks: *Neolepton georgianum* new species resembles *Neolepton lupei* in shell outline, differing by its smaller, higher, and more inequilateral shell. Hinge teeth, particularly the cardinal 1, are more delicate in *N. georgianum* than in *N. lupei*. The color of periostracum, pinkish in *N. georgianum* and whitish in *N. lupei* is also a distinctive character. *Neolepton georgianum* is also similar to *Neolepton holmbergi* new species, from which it differs in having a less inflated shell, shell outline with a pointed anterior end, and smooth shell surface. Both species are characterized by their pinkish periostracum.

Neolepton georgianum differs from *N. cobbi*, *N. Bennetti*, and *N. concentricum* by its quite ovate shell outline and smooth shell surface; the more inequilateral shell and the lower and not prominent beaks clearly separate *N. georgianum* from *N. falklandicum*. *Neolepton georgianum* also differs from *N. powelli* in having a more ovate shell outline, a consistently more acute anterior end and more curved dorsal and ventral margins. *Neolepton powelli* was described from Macquarie Island; in the same paper Dell (1964) also referred several specimens from South Georgia Islands to this species. Taking into account the narrow distribution ranges that characterize many *Neolepton* species, as inferred from the generic revision by Salas and Gofas (1998), it is not unlikely that the specimens from South Georgia Islands



Figures 11–18. *Neolepton holmbergi* new species. **11.** Holotype (MLP 6734-1), lateral view of the left valve. **12–18.** Paratype (MLP 6734-2). **12.** Posterior view. **13.** Detail of the protoconch. **14.** Shell surface sculpture. **15.** Inner view of a left valve. **16.** Inner view of a right valve. **17.** Left valve: detail of hinge. **18.** Right valve: detail of hinge. Scale bars: Figures 11, 12, 15–18 = 1 mm; Figures 13, 14 = 100 µm.

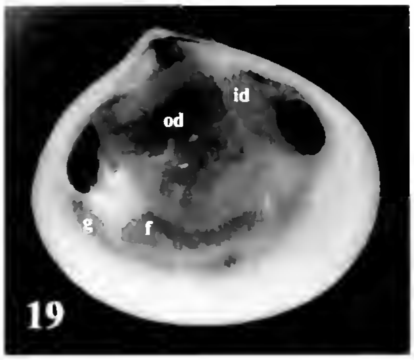


Figure 19. *Neolepton holmbergi* new species. A partially dissected specimen (L = 2.7 mm) showing details of soft parts anatomy. **f:** foot; **g:** gland cells of the mantle edge; **id:** inner demibranch; **od:** outer demibranch.

reported by Dell (1964) as *N. powelli*, would represent a different *Neolepton* species, possibly *N. georgianum*.

Neolepton holmbergi new species
(Figures 11–18)

Description: Shell delicate, small sized (maximum L = 2.8 mm), somewhat inflated (ratio W/H = 0.66 ± 0.03, n = 14), shell outline ovate, somewhat elongate, high (ratio H/L = 0.85 ± 0.02, n = 14), somewhat inequilateral, posterior end expanded, larger than anterior one; dorsal margin extended in a wide curve, tending to be straight at posterior half; posterior margin curved, ventral margin evenly arcuate, anterior margin short and curve. Beaks subcentral, usually eroded. Protoconch well-marked, smooth, not inflated, about 300 µm long. Shell surface dull shining or silky, sculptured with well-marked commarginal ribs, evenly spaced; periostracum pinkish.

Hinge plate solid, narrowing moderately below the beaks and at posterior half. Left valve: cardinal 2a relatively long, slender, enlarged at posterior end; cardinal 2b solid; posterior lateral PII elongated, hardly discernible from dorsal margin. Right valve: cardinal 1 high, with sharply triangular distal cusp and large base; 3a slender, long and low, 3b quite short, weak, PI well developed, elongate, with distal cusp.

Inner and outer demibranchs present: the outer much shorter, slightly overlapping the inner one and representing about the third of its length. Filaments of outer demibranch nearly horizontal. Inhalant aperture and exhalant siphon bordered by a single row of short tentacles. Glandular cells of the mantle edge present at both sides of the pedal aperture.

Type Material: Holotype, MLP 6734-1; paratypes: 20 MLP 6734-2, 10 MACN 35291, 10 MNHN unnumbered; all from the type locality, 8 April 1996, R/V Eduardo L. Holmberg.

Other Material Examined: (60 specimens from the type locality (MLP 6734-3, MACN 35292).

Type Locality: 54°18′ S, 35°30′ W, South Georgia Islands, 94 m.

Distribution: The species is only known from the type locality.

Etymology: The species is named after the R/V Eduardo L. Holmberg, aboard of which this species was collected.

Remarks: The general shell outline and the shell surface sculpture of well-marked commarginal regularly spaced ribs are diagnostic features of *Neolepton holmbergi* new species. *Neolepton holmbergi* is most similar to *Neolepton georgianum* new species, differing in having a more inflated shell, not much inflated protoconch and shell surface with stronger and regularly spaced commarginal ribs. The more triangular shell outline with nearly equally arcuate anterior and posterior ends is also distinctive for *N. holmbergi*. The hinge in *N. holmbergi* differs in having a high cardinal 1, with a wider base and triangular distal cusp.

Neolepton lupei, another similar species, clearly differs from *N. holmbergi* by its larger size, smooth shell surface, stronger hinge teeth and whitish periostracum.

Neolepton holmbergi differs from *Neolepton falklandicum* by its well-marked shell surface sculpture and not prominent beaks. *N. holmbergi* differs from the other Magellanic *Neolepton* species (*N. cobbi*, *N. concentricum* and *N. bennetti*) in being smaller, having a relatively lower and markedly ovate shell outline.

ACKNOWLEDGMENTS

The authors wish to thank A. Warén and K. Sindemark (SMNH) for allowing the study of types of *Neolepton lupei*, and K. Way and A. Campbell (NHM) for sending photographs of the holotype of *N. powelli*. D. Nahabedian kindly made available the specimens collected by the R/V Eduardo L. Holmberg. The authors are members of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work was partially supported by a grant from Fundación Antorchas to D. Z.

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A new species of *Metula* (Gastropoda: Colubrariidae) from the Lower Miocene Chipola Formation of Florida

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ABSTRACT

Metula miocenica, a new species described from the Lower Miocene Chipola Formation of northern Florida, is known only from the holotype that was extracted from an ancient reef deposit along Tenmile Creek in Calhoun County. Comparison of the new species reveals similarities with fossil congeners *Metula juncea* (Solander, 1766) from Eocene deposits of England and *Metula pilsbryi* Olsson, 1942, from the Plio-Pleistocene Charco Azul Group of western Panama and Costa Rica.

Additional key words: Buccinoidea, Neogene, Tertiary, fossil.

INTRODUCTION

A number of Recent and fossil species of the genus *Metula* are recorded from around the world, but most are rare. With few exceptions, nearly all living species occur in deep-water environments. The oldest known *Metula* comes from the Eocene, but most of the reported fossil species come from the late Tertiary. In Florida, two species occur in Neogene deposits. *Metula roberti* Olsson, 1967, has been collected from the Pliocene Pinecrest beds (upper Tamiami Formation) along the Kissimmee River and from quarries in Sarasota County, and a second species, described herein, has been recently discovered in the Lower Miocene Chipola Formation in northern Florida. The new species was collected from an ancient reef environment along Tenmile Creek in Calhoun County.

Type and figured specimens referred to in this paper are deposited in the Invertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida (UF), Gainesville.

SYSTEMATICS

Family Colubrariidae Dall, 1904
Genus *Metula* H. and A. Adams, 1853
Subgenus *Metula* H. and A. Adams, 1853

Metula (Metula) miocenica new species
(Figure 1)

Description: Shell elongate-fusiform. Protoconch glossy, 2 1/2 whorls. Teleoconch whorls 7, slightly convex. First two whorls with cancellate sculpture, axial sculpture becoming prominent on third and fourth whorls and with 2 to 3 distinct beaded spiral cords appearing below suture. Surface of remaining whorls generally smooth, exhibiting only very faint cancellate pattern, and spiral cords below shell suture losing their beaded sculpture. Aperture narrow, elliptical, slightly less than 1/2 shell length. Posterior portion of aperture attenuated, anal canal region slightly raised, with lirations on inner surface of outer lip. Columella and parietal wall of aperture with callus wash.

Type Material: Holotype, UF 110275, length 24.2 mm, width 8.0 mm.

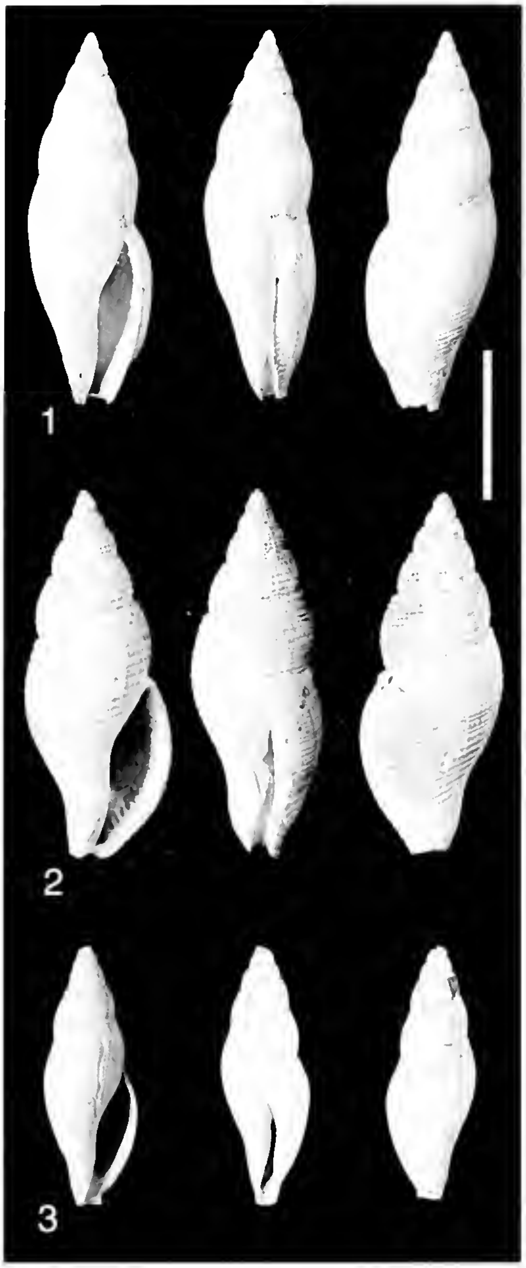
Type Locality: Tenmile Creek, about 0.78 kilometers west of Chipola River (SE1/4, Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 951), Chipola Formation.

Distribution: Known only from the type locality.

Etymology: Named for the epoch from which the species was collected.

Discussion: The oldest species of the genus *Metula* in the United States come from Eocene deposits in Maryland (Clark and Martin, 1901) and Mississippi and Louisiana (Palmer and Brann, 1966). There are no recorded specimens of *Metula* from the Eocene or Oligocene of Florida. Different species of *Metula* have also been recovered from Eocene deposits in France and England. For comparison purposes a specimen of *Metula juncea* (Solander, 1766) from the Upper Eocene Barton Beds in Hampshire County, England is illustrated (Figure 3) below the newly described *Metula (Metula) miocenica* (Figure 1). The similarity in sculpture and shape between *M. juncea* and *M. (M.) miocenica* and to other fossil and Recent *Metula* found in the Caribbean suggests an evolutionary linkage between the European and New World species.

Neogene *Metula* are known from numerous locations including New Hebrides (Ladd, 1976; 1982), Fiji (Ladd, 1977), Trinidad (Jung, 1969), Costa Rica (Olsson, 1922;



Figures 1–3. Florida fossil *Metula* and an Eocene counterpart from England. **1.** *Metula miocenica*, new species. Holotype, UF 110275, length 24.2 mm, width 8.0 mm. **2.** *Metula roberti* Olsson, 1967. Selected specimen from Kissimmee Canal, UF 62412, length 23.8 mm, width 9.5 mm. **3.** *Metula juncea* Solander, 1766. Selected specimen from Barton Beds, England, UF 1228, length 17.2 mm, width 6.2 mm. Scale bar = 10 mm.

1912), Panama (Woodring, 1964), Dominican Republic (Maury, 1917), and southern Florida (Olsson, 1967). Until now, the earliest Neogene species reported was by Woodring (1964) from the Lower Miocene Culebra Formation of Panama. That species was identified from "molds and incomplete impressions" and bore some resemblance to *Metula cancellata* Gabb, 1873. Because of the paucity and incompleteness of material, however, Woodring never described the Panama species.

Olsson and Bayer (1972) divided American *Metula* into several subgenera. In the largest subgenus, *Metula sensu stricto*, they placed those shells that possess an attenuated posterior aperture and long anal canal bordered by a lirated hump on the inner surface of the outer lip. Other members of the genus that lack the aforementioned features were either assigned to their new subgenera *Agassitula* or *Minitula*. The anterior canal of *Agassitula* is long and curved or twisted, whereas the anterior canal of *Minitula* is short and straight. Olsson and Bayer (1972) also named a fourth subgenus, *Floritula*, but were uncertain about its validity. The only known representative of this subgenus is the Florida Pliocene species *Metula roberti* Olsson, 1967. Since there are only trivial differences between the subgenera *Floritula* and *Metula* described by Olsson and Bayer (1972), Beu and Maxwell (1987) listed *Floritula* as a synonym for *Metula*. They also reclassified *Metula* (*Minitula*) *minor* Olsson and Bayer, 1972, the type species of the subgenus *Minitula*, into the family Columbellidae. Because of the attenuated posterior aperture and lirations on the inner surface of the outer lip, the Chipola *Metula* is assigned to the subgenus *Metula*.

There has been considerable uncertainty about the correct family classification of *Metula*. In a review of this controversy, Bouchet (1988) noted that some investigators opted to keep the genus in the family Buccinidae, while others felt that certain anatomical features of the radula justified assignment to the family Colubrariidae. Beu and Maxwell (1987), in an extensive revision of the *Colubraria* and related genera, classified *Metula*, *Colubraria*, and several related genera in the subfamily Pisaniinae into the Buccinidae. Vermeij (2001), in his review of the subfamily Pisaniinae, supported the placement of *Metula* in the Colubrariidae, which he maintained as a separate family near Buccinidae. His decision was based upon anatomical characteristics, shell morphology, and ecological factors. Commensurate with his findings, herein we follow Vermeij's assignment.

Metula (*Metula*) *miocenica* comes from the Lower Miocene Chipola Formation, which has an age range of 18 to 19 million years (Jones et al., 1993). Therefore, this newly discovered species is the oldest Neogene *Metula* thus far reported. In overall form it bears a stronger similarity to *M. juncea* from the Upper Eocene Barton Beds of England (Figure 3) than to the more recent Florida Pliocene species *Metula* (*Metula*) *roberti* (Figure 2). Among Neogene species, *M.* (*M.*) *miocenica* is similar to *Metula* (*Metula*) *pilsbryi* Olsson, 1942, from the Plio-Pleistocene Charco Azul Group in western Panama and Costa Rica. However *M.* (*M.*) *miocenica* is about half the size of *M.* (*M.*) *pilsbryi* and lacks the well-defined cancellate sculpturing on all but the first two whorls of the teleoconch. *Metula* (*M.*) *kerensis* Ladd, 1976, from Pleistocene deposits in New Hebrides is also similar to *M.* (*M.*) *miocenica*. Both have approximately the same shell dimensions and contours and both possess a very faint cancellate sculpture on the later whorls. However, *M.* (*M.*) *miocenica* has two to three prominent spiral bands that appear just below the sutures and in the early whorls there is also a more prominent cancellate sculpture pattern. Among extant Caribbean species *M.* (*M.*) *miocenica* is most similar to *Metula* (*Metula*) *ellena* Olsson and Bayer, 1972. Both have approximately the same body dimensions and shape and both have fine to smoothly cancellate body sculpturing. *Metula* (*M.*) *miocenica*, however, is more slender, has a more elevated spire, and the body whorl is more sharply angled toward the base.

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A new species of Ancillariinae (Gastropoda: Olividae) from the southwestern Atlantic Ocean

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ABSTRACT

A new species of the ancillid genus *Amalda* is described from the southwestern Atlantic off Brazil, Uruguay, and Argentina. *Amalda josecarlosi* new species was identified as *Ancilla dimidiata* and *A. tankervillii* by previous authors. Detailed study of the type material and other specimens of the two latter taxa allowed for the recognition of the new species. Adults and juveniles of *Amalda josecarlosi* new species from several localities along the Southwestern Atlantic coast are illustrated, described and compared to other living congeners.

INTRODUCTION

The genera *Amalda*, *Ancilla*, and several other Ancillariinae from the southeastern Atlantic were thoroughly studied by Kilburn (1977, 1980, 1981, 1993). Kilburn and Bouchet (1988) also studied the genus *Amalda* from New Caledonia describing four new species and one subspecies. Besides *Amalda josecarlosi* new species, there are four species of Ancillariinae in the southwestern Atlantic: *Ancilla faustoi* Matthews, Matthews and Dijck, 1980, *A.* (*Hesperancilla*) *matthewsi* Burch and Burch, 1967 and *Eburna lienardii* (Bernardi, 1859). *Amalda tankervillii* (Swainson, 1825) occurs only off northern South America (*i.e.* Isla Margarita, Venezuela). Rios (1994) expressed doubts about the presence of this species off Brazil. There is not, however, a systematic treatment of the subfamily for the species occurring in the southwestern Atlantic.

Dall (1890) mentioned young and dead specimens of *Amalda tankervillii* off Río de La Plata (Argentina) and the Brazilian coast collected by the ALBATROSS expedition at stations 2764 and 2762, respectively. Perhaps influenced by the latter record, Fernández (1965) also cited *Ancilla tankervillii*, a Venezuelan species and type of the genus *Amalda* H. and A. Adams, 1854, from off Argentina. Scarabino (1977) considered this record as *Ancilla dimidiata* and extended the known range of this species to San Matías Gulf, Río Negro Province, Argentina (~41°S). Previously, Strebel (1908), based on material of the Swedish Südpolar Expedition, illustrated what he identified as *A. dimidiata* from the southern coast of the Brazilian state of Rio Grande do Sul. Marcus and Marcus (1968) studied the anatomy of specimens supposedly of *Ancilla dimidiata* but based the name on specimens identified by Klappenbach from the littoral of Rio de Janeiro State, Brazil (Ubatuba and Angra dos Reis). The specimens studied by Marcus and Marcus are herein assumed to belong to the new species.

In his original description of *Ancillaria dimidiata*, G. B. Sowerby II (1859), gave Red Sea as the type locality. Later, E. A. Smith (1915: 96) challenged that locality and mentioned that G. B. Sowerby III's record (1892) of *A. dimidiata* from South Africa was probably incorrect. This latter opinion was confirmed by Kilburn (1981: 408) who synonymized *A. dimidiata* (G. B. Sowerby III, 1892; non G. B. Sowerby II, 1859) with *Ancilla marmorata* (Reeve, 1864). The present report includes, in addition to the description of the new species of *Amalda*, a study of the syntypes of *Ancillaria dimidiata* G. B. Sowerby II, 1859, the holotype of *Ancillaria tankervillii* Swainson, 1825, and several other relevant lots of these species.

MATERIALS AND METHODS

The specimens examined in this study are deposited in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), Museo de La Plata, La Plata, Argentina (MLP), and the Museo Nacional de Historia Natural Montevideo, Uruguay (MNHNM). Two syntypes of *Ancillaria dimidiata* and the holotype of *Ancillaria tankervillii* are housed in The Natural History Museum, London (BMNH), BMNH 197832 and BMNH 197824 respectively. Reference material from Brazil housed at the Museu de Zoologia de la Universidad de São Paulo, Brazil (MZSP) and at the J. C. Tarasconi collection (Porto Alegre, Brazil) were also studied.

Dissections were performed on ethanol-preserved specimens. The radulae were prepared according to the method described by Solem (1972). Most photographs were taken using a digital camera. All images were digitally processed.

Most of the terminology used in the description of the species followed Kilburn (1977, 1981), Marcus and Marcus (1968), and Voskuil (1991). However, the **posterior groove** (apical line of Marcus and Marcus, 1981) is here defined as the narrow and weak groove of the last whorl, which starts in the parietal callus, runs parallel to the ancillid groove, and ends in the labrum. The area between the posterior groove and the ancillid groove is here referred to as the **last whorl middle band.** A data matrix based on 26 shells was prepared including their maximum length and width and the length of the region between the posterior groove and the ancillid groove when both grooves reach the edge of the labrum (see Table 1). Figures 22–25 show the different shell terminologies.

SYSTEMATICS

Class Gastropoda Cuvier, 1791
Order Neogastropoda Wenz, 1938
Family Olividae Latreille, 1825
Subfamily Ancillariinae Swainson, 1840

Remarks: I follow Kantor and Bouchet (1999), who showed that Ancillariinae Swainson, 1840, has priority over Ancillinae H. and A. Adams, 1853.

Genus *Amalda* H. and A. Adams, 1853

Type Species: *Ancillaria tankervillii* Swainson, 1825, by subsequent designation of Vokes, 1939.

Amalda josecarlosi new species
Figures 1–14

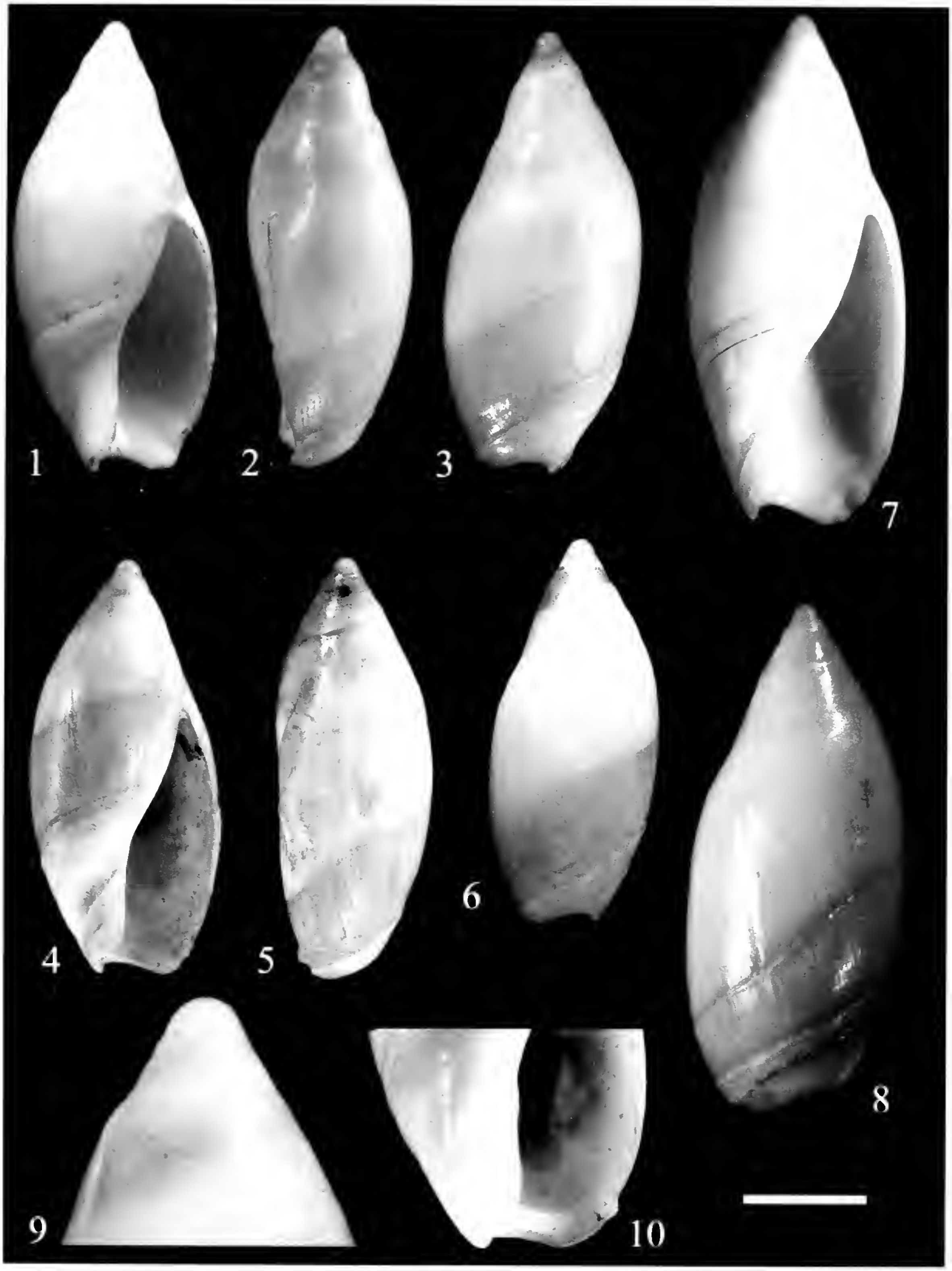
Ancillaria tankervillei Dall, 1890: 310.
Ancillaria dimidiata Strebel, 1908: 25, pl. 1, figs. 2a–c.
Ancilla dimidiata Smith, 1915 *non* Sowerby, 1859, *nec* Sowerby, 1892; Marcus and Marcus, 1968, figs. 1–9 (anatomy); Rios, 1970: 102, pl. 32; 1975: 111, pl. 33, fig. 472; 1985: 111, pl. 38, fig. 491; 1994: 143, pl. 46, fig. 613; Figueiras and Sicardi, 1973: 264, pl. 15, fig. 193; Scarabino, 1977: 191, pl. 3, fig. 8; Calvo, 1987: 164, fig. 148.
Ancilla tankervillei Fernández, 1965: figs. 1–4; Castellanos, 1970: 121, Pl. 9, fig. 7 *non* Swainson, 1825.

Diagnosis: Shell small, elliptic ovate. Spire low, covered by primary callus, secondary callus tongue-shaped, aperture thin, with labral denticle subterminal, conspicuous. Columellar pillar straight, 3–4 oblique pleats, posterior groove starting at the parietal callus, slightly adapical to the posterior angle, ending gradually below the middle part of labrum. Adult specimens show sudden change in direction of posterior groove toward anterior edge of labrum. Shell bright-white, adult specimens with faint darker subsutural line visible under spire glaze and comprising a region delimited by the posterior groove and the ancillid groove; last whorl middle band darker

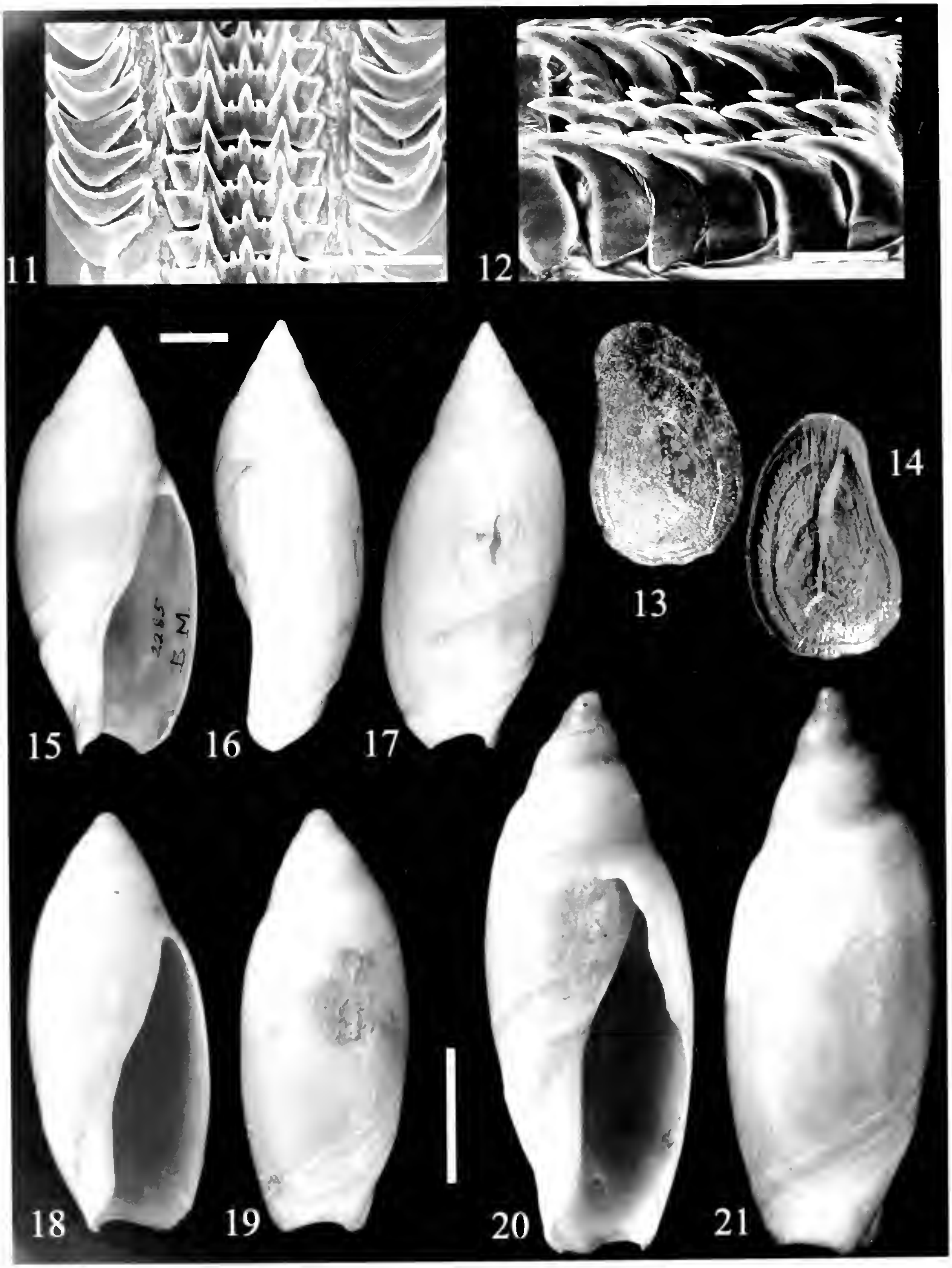
Table 1. Shell measurements (mm) of *Amalda josecarlosi* new species and *A. dimidiata* syntypes.

Amalda josecarlosi new species	Shell length	Shell width	Posterior groove last whorl middle band
MACN 6519			
Holotype	17.6	8	3.7
MACN 23489			
Paratype	18.8	8.6	3.9
	17	7.6	4.8
MACN 9361-57			
Paratype	10.8	4.6	3
MACN 10295	20.8	9.2	4.2
MACN 15356			
Paratype a	15.4	7	2.5
Paratype b	15.6	6.8	3.7
Paratype c	9.8	4.9	3.5
MACN 8587-16			
Paratype a	16	7.6	3
Paratype b	13.2	6.4	3.1
MACN 10707			
Paratype	13.3	5.8	3.2
MLP 1454			
Paratype	17.4	8.2	1.8
Tarasconi collection (Santa Catarina)			
Specimen a	12.2	5.6	3.2
Specimen b	12	5.6	2.3
Specimen c	11.7	5.2	2.4
Specimen d	9.6	4.4	2.7
Tarasconi collection (São Paulo)			
Specimen a	12.8	5.8	3.6
Specimen b	10.3	4.9	3.3
Specimen c	10	4.6	2.4
Specimen d	7.4	3.4	1.2
MLP s/n	21	9.3	2.4
MZSP 32883	11.7	5	3.3
Specimen a	9.1	3.6	2.8
Specimen b	9	4	2.8
A. dimidiata			
Syntype 1	20.6	7.8	8.5
Syntype 2	15.8	6.5	7.5

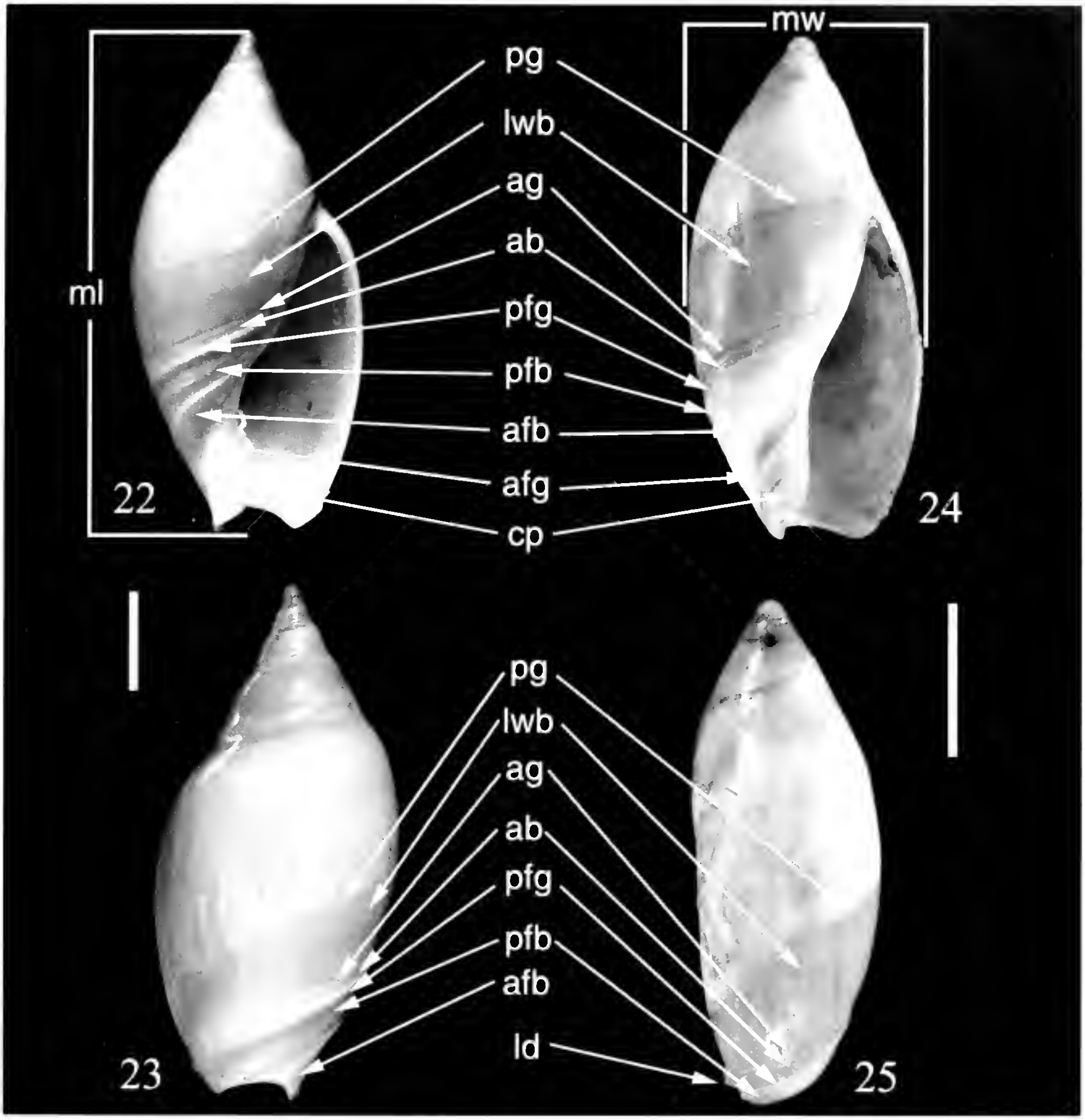
Description: Shell small, up to 22 mm in length, elliptic-ovate, somewhat fusiform, with five smooth, flat whorls. Protoconch with 2.5 whorls, completely smooth, translucent. Suture impressed, visible only in the first whorls of young specimens, covered in adult specimens by primary callus, except on protoconch. Secondary tongue shape callus extends from the middle of the penultimate whorl, over the posterior angle of the aperture and the posterior part of the labrum, to the beginning of the columellar pillar. Last whorl slightly shouldered. Aperture triangular, posterior end strongly angled, la-



Figures 1–10. *Amalda josecarlosi* new species. **1–3.** Holotype, MACN 6519, Golfo San Matias, Rio Negro, Argentina. **4–5.** Paratype, MACN 8587-16, ARA Patria, Station 80, off Mar del Plata, Buenos Aires. **6.** Paratype, MACN 15356-1, 34°40′ S-53°59′30″ W. **7–8.** MLP unnumbered, Mar del Plata, Buenos Aires. **9.** Detail of the protoconch of the specimen of fig. 4–5. **10.** Detail of the basal part, showing the labral denticle. Scale bar = 5 mm for Figures 1–8.



Figures 11–21. **11–12.** *Amalda josecarlosi* new species. **11.** Dorsal view of the radula. Scale bar = 50 µm. **12.** Lateral view of the same radula. Scale bar = 20 µm. **13–14.** External and internal views of the operculum. Scale bar = 2.5 mm. **15–17.** *Amalda tankervillii* (Swainson, 1825), three views of the holotype BMNH 197824. Scale bar = 10 mm. **18–21.** *Ancillaria dimidiata* Sowerby, 1859, two views of the two syntypes BMNH 197832. Scale bar = 5 mm.



Figures 22–25. **22–23.** *Amalda tankervillii* (Swainson, 1825) from Isla Margarita, Venezuela. Scale bar = 10 mm. **24–25.** *Amalda josecarlosi* new species, MACN 8587-16, off Mar del Plata, Buenos Aires. Scale bar = 5 mm. Abbreviations: ab: ancillid band; afb: anterior fasciolar band; afg: anterior fasciolar groove; ag: ancillid groove; cp: columella pillar; ld: labral denticle; lwb: last whorl middle band; ml: maximum length; mw: maximum width; pfb: posterior fasciolar band; pfg: posterior fasciolar groove; pg: posterior groove.

brum very thin, sharp, curved; basal denticle subterminal, conspicuous; labral base projects beyond base of columella base. Siphonal notch deep. Columellar pillar straight, with 3–4 oblique pleats, the posterior larger reaching the parietal callus; anterior fasciolar groove fairly deep; anterior and posterior fasciolar band ("opaque area" of Marcus and Marcus, 1981) of similar width and divided by a weak median ridge; posterior fasciolar groove very weak. Posterior groove starting slightly above the posterior angle of the aperture and ending gradually always abapically to the middle part of labrum. Adult specimens show sudden change of direction of posterior groove toward the anterior edge of the labrum (Figure 5). Ancillid groove shallow, ancillid band narrow

Growth lines covering entire shell, very conspicuous on last whorl, forming a brown color pattern. "Microshagreen" sculpture ("microscopic pustules" *sensu* Kilburn, 1981) regularly packed in both calluses and less dense on columellar pillar and adapertural part of labrum. Color bright white; some specimens (usually adults) with a subsutural dark but faint line under spire glaze. Region delimited by the posterior groove and the ancillid groove ("basal groove" of Marcus and Marcus, 1968, herein referred to as "last whorl middle band") brownish or dark tinted. Operculum delicate, pale-yellow, ovate-elliptical, somewhat oblong, nucleus subterminal, attachment area on left side (Figures 13–14).

Radula is rachiglossate; rachidian teeth with three cusps, the central one shorter than the laterals. One denticle between the central cusp and the laterals (sometimes an extra obsolete, asymmetric denticle is visible, see Figure 12), always rising from the base of the rachidian tooth. Marginal teeth curved with a thick attachment area.

It is interesting to remark that the short central cusp of the rachidian in radula is a recurring character in the genus *Amalda* (as far as it can be seen on *A. lemaitrei*, *A. crosnieri* and *A. jenneri*, all Kilburn, 1977). However *Ancilla (Hesperancilla) matthewsi* Burch and Burch, 1967 (according to Kilburn, 1981:450 figure 239) has also the same kind of rachidian teeth. The full significance is unknown.

Type Material (Table 1): Holotype: MACN 6519, P. H. Bruno Videla and A. Pozzi coll., May 1946, dead shell. Paratypes: two shells, MACN 23489, 34°40′ S–58°18′ W, 100 m depth, 18 Sep.1938, one shell, MACN 9361-57, Mar del Plata, Mar. 1915; two shells + one live-collected specimen, MACN 15356-2, 34°40′ S–53°59′30″ W, 29.3 m depth, Mar. 1925; one shell, MACN 8587-16, ARA (research vessel) PATRIA, Station 80, off Mar del Plata; one shell, MACN 10707, Mar del Plata; one shell, MLP 1454, Miramar, Buenos Aires; one shell, MNHNM 9111, Cabo Polonio, Departamento Rocha, Uruguay, fishing boat, 3 Nov. 1958.

Type Locality: Golfo San Matías, Río Negro Province, Argentina (~41° S).

Other Material Examined: One shell, MACN 10295, Mar del Plata, Buenos Aires; one live-collected specimen, MLP unnumbered, Mar del Plata (Figures 7–8) (this is probably the same specimen mentioned and dissected by Fernández, 1965; she did not, however, report the collection number and, as far as information on the label goes, the material has no special nomenclatural standing); four live collected specimens, Tarasconi collection, southern coast of São Paulo State, Brazil, 20–40 m depth, December 1996; five live-collected specimens, Tarasconi collection, off Laguna, Santa Catarina State, Brazil, 60–80 m depth, Apr. 2000; three live collected specimens, MZSP 32883, off Angra dos Reis, Rio de Janeiro State, Brazil, Mar. 1969.

Distribution: From Espirito Santo, Brazil (Rios, 1994) (~20° S) to Golfo San Matías, Argentina (~41° S) (Scarabino, 1977). The depth range appears to increase from the north, where it is a shallow water species, to the south, where it lives in depths to 80 m.

Etymology: Named after my friend and serious collector José Carlos Tarasconi from Porto Alegre, Brazil.

Comments on Literature Records: Strebel (1908: 33°05′–51°10′ W (south of Rio Grande do Sul State, Brazil), 80 m depth, station 1 of the Swedish Südpolar Expedition, as *Ancilla dimidiata*); Scarabino (1977) cited this species (also as *Ancilla dimidiata*) from off Bahía San Antonio, Golfo San Matías (~41° S) in sandy bottoms. Dall's material from the Albatross expedition originally identified as *Ancillaria tankervillii* (*A. tankervillei* of Dall) and later identified by M. A. Klappenbach as *Ancilla dimidiata* (Y. Kabat pers. comm.): USNM 96128, Station USFC 2762, 111.6 m depth, 20°08′ S, 41°34′ W (30 Dec. 1887); USNM 96619, Station USFC 2764, 21.0 m depth, Samborombón Bay, 36°42′ S, 56°23′ W (12 Jan. 1888) both stations published in Dall (1890); and USNM 224495 and 686371 are from station USFC 2766, 19.2 m depth, Samborombón Bay, 36°47′ S, 56°23′ W (12 Jan. 1888) (Kabat, pers. comm.).

DISCUSSION

Amalda josecarlosi new species was confused with *A. dimidiata* and *A. tankervillii* by various authors (Dall, 1890; Strebel, 1908; Fernández, 1965; Castellanos, 1970; Scarabino, 1977; among others). Kilburn (1977) provided a short diagnosis of the genus *Amalda* that was adopted herein, however, the definition of a new character was necessary in order to clarify the shell morphology of the new species as well as the type. Subgeneric assignment was avoided because as Kilburn remarked subgenera "are in urgent need of revision".

Amalda tankervillii (Figures 15–17) from Venezuela, mentioned by Dall (1890) from off Río de la Plata and erroneously identified by Fernández (1965), is a species large for the genus, which reaches more than 75 mm, with an almost smooth columella pillar and a thin fringe between the posterior groove and the ancillid groove, defined here as the last whorl middle band. Coloration is also very different: distinct shades of pale orange for *A. tankervillii* and whitish for the new species. Dall (1890), Fernández (1965), and Marcus and Marcus (1968) among other authors, used an emended version of the spelling of this species: *A. tankervillei*. However, according to the Articles 32.3 and 32.5 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) the original incorrect latinization is not considered an error and therefore does not warrant emendation.

Two syntypes of *A. dimidiata* housed at the BMNH apparently have never been illustrated after the original description. Unfortunately, soft parts were not preserved. They are similar to the new species here described but it has a thinner profile, the columella pillar

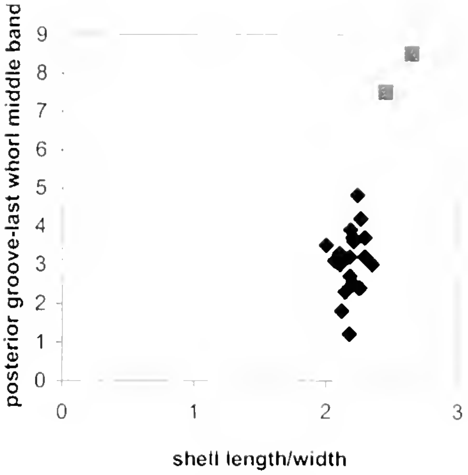


Figure 26. Scatter diagram showing the relation between length of the field between the apical line and ancillid band vs. shell length/width of *Amalda josecarlosi* new species (◆) and syntypes of *Ancilla dimidiata* (■). N = 20

is straighter and with less conspicuous plaits, and the anterior fasciolar groove is deeper. The posterior groove in both syntypes of *A. dimidiata* always reaches the labrum above its middle point. On the other hand, in all the specimens studied (more than 20 at different ontogenetic stages and from different localities), the apical line of the new species always reaches the labrum anterior to its middle point, particularly in adult specimens. The scatter diagram (Figure 26) showing a plot of the length of the last whorl middle band at the edge of the labrum (the band between the posterior groove and ancillid groove) vs. the shell length/width clearly shows the difference between the two syntypes of *A. dimidiata* and several specimens of *A. josecarlosi* new species. As far as I know, the geographical distribution of *A. dimidiata* does not include waters off Argentina. Due to the large and poorly explored Brazilian shelf, its presence or absence off this country could not be verified. Kilburn (pers. comm.) considered the Red Sea as an erroneous locality. The real range of *A. dimidiata* remains uncertain.

Voskuil (1991) redescribed and illustrated the recent species of the genus *Eburna* Lamarck, 1801, including two species from the southern Caribbean, *E. glabrata* (L., 1758) (type species of *Eburna*) and *E. balteata* (Swainson, 1825) and one from off northern Brazil, *E. lienardii* (Bernardi, 1859). In addition, Kilburn discussed the diagnostic characters of the genus *Amalda*. He pointed out the definition of *Amalda* of some recent authors better fits some species of *Baryspira* than *A. tankervillii*, type species of *Amalda*. According to Voskuil (1991) the diagnosis of *Amalda* followed by Chavan (1965) and Kilburn (1977) was based on species of *Baryspira* rather than on *A. tankervillii*. Voskuil finally concluded that *Amalda* should be considered as a subgenus of *Eburna*. I agree that the *Amalda* species described by Kilburn and Bouchet (1988) and Kilburn (1993) present several distinct characters that are somewhat far removed from those in *A. tankervillii*. Perhaps future research will show that *Amalda* deserves further taxonomic division.

The morphology of the umbilicus of the species included in *Eburna* are in fact a conclusive character that should warrant full generic status. However, *Amalda* (type species *Amalda tankervillii*) should also be considered as a full-fledged genus with two species in the southwestern Atlantic.

According to the literature, most of the species of Ancillariinae occur outside the New World. South Africa, the Arabian Peninsula, New Caledonia, and Indonesia appear to be the regions with the largest number of species. *Amalda josecarlosi* new species is the only species of the subfamily living in Argentina. In addition, despite the good development of Tertiary deposits in Patagonia, there is no record of fossil representatives of this genus. Therefore, *Amalda josecarlosi* new species, the southernmost living species of the subfamily, is probably derived from the Caribbean stock in which area the type species of the genus presently occur.

ACKNOWLEDGMENTS

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On the publication date, authorship, and type species of *Umbraculum* and *Tylodina* (Gastropoda: Opisthobranchia: Tylodinoidea): a rejoinder

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ABSTRACT

Further review of the literature reveals that type designations earlier than, or different from, those proposed by Valdés (2001) are available for *Umbraculum* Schumacher, 1817, and three of its synonyms *Umbrella* Lamarck, 1819, *Gastroplax* Blainville, 1819, and *Ombrella* Férussac, 1822. The type species of *Umbraculum* is *U. chinense* and the specific name should be attributed to Lamarck, 1801 (who called it *Umbella chinensis*). This species is a junior synonym of *Patella umbraculum* [Lightfoot, 1786], a name introduced in an anonymous work. The neuter gender of *Umbraculum* must be reflected in the names of attributed species. Rafinesque's descriptions of his genera *Tylodina* and *Oxynoe* are reproduced from his 1814 work. In the interests of nomenclatural stability, it is recommended that Umbraculoidea be accorded the status of *nomen protectum* (in favour of Tylodinoidea) for the monophyletic higher taxon (with the rank of superfamily in a Linnaean hierarchy) encompassing the families Umbraculidae and Tylodinidae.

INTRODUCTION

Stimulated by the recent synthesis by Angel Valdés (2001) of nomenclatural problems associated with the genera *Umbraculum* and *Tylodina*, the present paper attempts to determine the valid name, exact dates of publication, and type species of these two molluscan genera and their synonyms. Close scrutiny of the literature reveals several earlier overlooked type designations, and provides a different interpretation of the correct name of the type species of *Umbraculum*. The original 1814 descriptions by Rafinesque of his genera *Tylodina* and *Oxynoe* are reproduced from this rare work. Adanson's (1757) "Le Liri" from Senegal, the basis of *Patella perversa* Gmelin, 1791, is briefly reviewed and commented upon.

DISCUSSION

UMBRACULUM: ITS TYPE SPECIES AND VALID NAME

Schumacher (1817) included only one species in his new genus *Umbraculum*, the "Parasol chinois" *Umbraculum chinense*. That is, the type species was clearly established by monotypy. Schumacher's text can be easily mis-read, as the genus is diagnosed on page 55 and described on page 177, with the type species designation on the top line of page 178 where it looks more like a running head rather than the first line of text for that page.

The question next to determine is to which author should the species name be attributed. Schumacher is the obvious choice as author of the species name *chinense* because it was he who correctly latinized and cited the "*Umbella chinensis*" of [the non-binominal] Chemnitz (1788) as first among his references. Indeed, both Pilsbry (1896) and Sherborn (1930) attributed the species name in the binomen *Umbraculum chinense* to Schumacher (1817). Harris (1897) went a little further, allocating authorship of the species name to "Schumacher (ex Martini)", that is Chemnitz (1788). However, to quote Valdés (2001: page 30), " '*Umbella Chinensis*' of Chemnitz (1788), was published in binominal form by Lamarck (1801) as *Umbella chinensis*" when Lamarck published it in the synonymy of his new species of supposed bivalve *Acardo umbella*. [Deshayes (1827) effectively removed *Acardo* from molluscan literature by pointing out that it was an "epiphise de vertèbres de Cétacés."] Nowadays, names first published in synonymy are not available (ICZN 1999, Article 11.6). If, however, a junior synonym introduced into the literature has been treated as an available name before 1961 and adopted as the name of a taxon, it is made available with author and date from its first introduction as a synonym (ICZN Articles 11.6.1 and 50.7). In this instance, *Umbella* was not adopted as the name of a taxon except by Delle

Chiaje (1831), d'Orbigny (1841, 1842) and Gray (1847), by which time *Umbraculum*, *Umbrella*, *Gastroplax* and *Ombrella* were its senior synonyms. The species name *chinensis* was adopted by Schumacher (1817), Pilsbry (1896) and Harris (1897) as a valid name, the authorship and date of which therefore should be Lamarck (1801). In conclusion, *Umbraculum chinense* (Lamarck, 1801) is the type species of *Umbraculum* by monotypy.

Valdés and Lozouet (2000) listed *Patella umbraculum* Lightfoot, 1786, as type species of *Umbraculum* by "absolute tautonomy". But, as the species name *umbraculum* is not identical in spelling with any of the five species cited by Schumacher (1817) in the synonymy of his new genus, i.e., *Umbella chinensis*, *Acardo umbella*, *Acardo orbicularis*, "*Parasol chinois*", *Patella umbellata*, type designation by absolute tautonomy cannot be correct. Curiously, because *P. umbraculum* is the type species by its seniority at the head of the list of synonyms, it has become type species by what may be termed subsequent tautonomy, a designation not covered by the Articles of the International Code of Zoological Nomenclature. Dall (1889) listed "*umbrella*" Gmelin, 1791, possibly a mistake for *umbellata* Gmelin, 1791, as type species of the genus, but no such species appears in Schumacher's (1817) work, thus invalidating this selection. Gmelin (1791) described species of *Patella* that he named *sinica* (page 3705) and *umbellata* (page 3720). Of these two, Schumacher included reference only to the latter. Dillwyn (1817) [as First Revisers of these two works published in the same year, we give precedence to Schumacher] preferred *Patella umbellata* Gmelin, 1791, as the name for this species, listing *P. sinica* as next in seniority. Pilsbry (1896) reversed the order, accepting the page priority of *P. sinica*. Dillwyn (1817) included *Patella umbraculum* [Lightfoot, 1786] (square brackets signify anonymity) in his published synonymy, but thereafter this species name was overlooked until the mid-20th century (Taki, 1951; Rehder, 1967). Pilsbry's (1896) selection of *P. sinica* as type species of *Umbraculum* is also invalid (Valdés, 2001).

UMBRACULIDAE AND *UMBRACULUM*: THE SYNONYMS

When Dall (1889) pointed out the priority of *Umbraculum* Schumacher, 1817, over *Umbrella* Lamarck, 1819, he also introduced the family name Umbraculidae, which today is in constant and consistent use by malacologists worldwide. Pilsbry (1896) was the first subsequent author to accept and use both *Umbraculum* and Umbraculidae. The earliest family name appears to be the vernacular "Les Ombrelles" of Férussac (1822), the formal latinization of which has never taken place. The first properly latinized family name was Umbrellidae by Gray (1827). Operculatinae was established by H. and A. Adams (1854). Dautzenberg and Bonge (1933) seem to have been the last authors to use Umbrellidae, though as late as 1951 Barnard still called the genus *Umbrella*.

Odhner (1939) created the subordinal rank Umbraculacea to include the two families Umbraculidae Dall, 1889, and Tylodinidae Gray, 1847. Names of higher rank than superfamily are not governed by the Code of Zoological Nomenclature (ICZN, 1999), therefore the correct authorship at subordinal rank is Umbraculacea Odhner, 1939. Ordinal rank has been accorded the group by Minichev and Starobogatov (1978) and by Hamatani (2000) with the names Umbraculida and Umbraculomorpha, respectively. When this higher rank name is ranked as a superfamily (i.e. Umbraculoidea), it is subject to the "Principles of Co-ordination" (ICZN, 1999, Article 36.1); though first assigned this rank by Morton (1958), its authorship is attributed to Dall (1889). Abbott (1974), with an eye to priority of the included families, altered the superfamily name to Tylodinacea. Vaught (1980) followed suit, but indicated Umbraculacea as an alternative. More recently, this name, now emended with the suffix –oidea, to Tylodinoidea, has been utilized (as a superfamily in ranked Linnaean classifications on three occasions, and as unranked in six phylogenetic classifications) by Willan (1998) and others (Tsubokawa and Miyazaki, 1993; Rudman, 1998–2002; Higo et al., 1999; Wägele and Willan, 2000, where the name was inadvertently misspelled Tylodinidoidea on page 91; Schrödl et al., 2001; Valdés, 2001; Wägele and Johnsen, 2001; Wollscheid-Lengeling et al., 2001). The clear majority of authors, however, have not followed Abbott's alteration, and have continued to use Umbraculoidea in one higher ranking form or another (i.e., Ros, 1975; Thompson, 1976; Marcus, 1977, 1983, 1984, 1985; Cernohorsky, 1978; Kay, 1979; Powell, 1979; Bertsch, 1980; Piani, 1980; Vaught, 1980, 1989; Eisenberg, 1981; Kilburn and Rippey, 1982; Willan, 1981, 1983, 1984, 1987; Cattaneo and Barletta, 1984; Healy and Willan, 1984; Schmekel, 1985; Cattaneo-Vietti, 1986; Hoisæter, 1986; Burn, 1989; Smriglio et al., 1990; Sabelli et al., 1990; Poppe and Gotto, 1991; Christiaens, 1991; Villani, 1991; Rosenberg, 1991; Tsubokawa and Miyazaki 1993; Rios 1994; Bosch et al., 1995; Mikkelsen, 1998; Wirtz, 1998, 1999; Valdés and Lozouet, 2000). So, in the interests of nomenclatural stability, it is advocated that Umbraculoidea be maintained as a *nomen protectum* (ICZN, 1999, Article 23.9.2).

As early as July 1823 (Children, 1823a, but no author's name appears on the actual work), and again later that same year (Children, 1823b), Children wrote: "*Umbrella* Type *Umbrella indica*. *Patella umbellata*, Gmel. Indian umbrella, commonly called the Chinese parasol." This type designation is valid, and must stand (Kennard et al., 1931). Children also directed attention to the synonymy of Lamarck's *indica* with the earlier *Patella umbellata* Gmelin, 1791. Pilsbry (1896) later selected the page prior *P. sinica* Gmelin, 1791 as the better name to use for this species. Page xxix of Férussac (1821–1822) appeared as part of livraison 15, published on 13 April 1822 (Kennard, 1942). *Ombrella* Férussac therefore dates to 1822; its type species, *Ombrella indica* (Lamarck, 1819), was subsequently designated by O'Donoghue (1929). Thus, the type designations by Valdés (2001) for *Umbrella* and *Ombrella* are both unnecessary.

O'Donoghue accepted *Operculatum* as a genus name introduced by H. and A. Adams (1854) and designated as type one of the included species, *O. mediterraneum* (Lamarck, 1819). However, it was Mörch (1852) who validly introduced this genus name, at which time *mediterraneum* was not among the original included species. Valdés (2001) rectified this situation by selecting *Umbrella indica* Lamarck (1819), one of the species listed, albeit as a synonym, in Mörch's paper. *Operculatum laeve*, a binomen originally used by Linnaeus (1753) in a non-binominal pre-Linnaean work, was, like *Umbella chinensis*, latinized and introduced in the synonymy of *Patella sinica* Gmelin (1791) by de Roissy (1804), and again in the synonymy of *Patella umbellata* Gmelin (1791) by Dillwyn (1817). Fortunately, the genus name was not adopted as a valid taxon except by Mörch (1852, 1875) and H. and A. Adams (1854), when it was already the junior synonym of *Umbraculum*, *Umbrella*, *Gastroplax*, and *Ombrella*. The specific name *laeve* has never been adopted, except by Mörch (1852).

Blainville (1819) included only the non-binominal species "*Patella ombracula Chemnitz*" in his new genus *Gastroplax*; in 1820 he Latinized the name as *Patella umbracula*. Chemnitz (1788) actually called his species "Der chinesische Sonnenschirm", and his Latin description read "*Umbella chinensis, testa integra, subrotunda, diaphana, albida, depressa, planiuscula, vertice luteo, cavitate lineis radiata, flavescente, margine acutissimo*". Nowhere does "*ombracula*" or *umbracula* appear. Whilst Blainville's generic description is valid (ICZN 1999, Article 12.2.7), inclusion of a non-existent species name from a non-binominal work does not constitute designation of a type species by monotypy, contrary to the statement of Valdés (2001). Unless, of course, *Gastroplax* and "*Patella ombracula*" could be considered as a combined description of a new nominal genus and single new nominal species (ICZN 1999, Article 12.2.6), in which case Blainville (1819) would be the author of both names. However, Blainville himself did not consider this to be the case, because in 1820 he named the species upon which he based his genus, *Gastroplax tuberculosus*, whereupon it became type species by subsequent monotypy (ICZN 1999, Article 69.3).

At the same time, Blainville (1820) introduced in synonymy the binomen *Patella umbracula*, attributing it to Chemnitz. *Patella umbracula* is both a primary homonym and junior synonym of *Patella umbracula* (Röding, 1798), and is of no further concern. Curiously Röding's (1798) authorship of the species name *umbraculum* has been unnecessarily revived by Sabelli et al. (1990).

The earliest available name for the type species of *Umbraculum* is *Patella umbraculum* [Lightfoot, 1786], introduced in an anonymous work, and it is generally accepted that all species names proposed for the "Parasol chinois" are synonyms (Rehder 1967). Lightfoot (1786) correctly combined *Patella*, feminine in gender, with *umbraculum*, neuter, as a noun in apposition. He did not write *Patella umbracula* as used by Valdés (2001), though this spelling was utilized in the early days by Röding (1798) and Blainville (1820). The genus name *Umbraculum* too is neuter in gender, hence its included species should all agree if the species names are adjectival in origin. The recently described fossil species *U. sanctipaulensis* Valdés and Lozouet, 2000, and the fossil species with which it is compared in that work, *U. laudunensis* (Melleville, 1843), for example, must be corrected to *sanctipaulense* and *laudunense* respectively.

Burn (1959) suggested that there is only one Recent, worldwide, pan-tropical/warm temperate species in the genus *Umbraculum*, but this hypothesis has yet to be tested. There are twelve Recent nominal species of *Umbraculum*. Marcus and Marcus (1967) and Marcus (1985) retained the name *U. plicatulum* (von Martens, 1881) for warm-water western Atlantic specimens, and Thompson (1970) *U. mediterraneum* (Lamarck, 1819) for those from the Mediterranean Sea. From the Oligocene beds of northern Germany, there has been described a somewhat doubtful fossil species *Umbrella? plicatula* von Koenen, 1892, which, if correctly assigned, would be a primary homonym of von Martens' species. *U. pulchrum* Lin, 1981, from Hainan Island, southern China, with no characters to separate it, is the most recent synonym of *U. umbraculum*.

In summary, the synonymy of *Umbraculum* now reads:

Umbraculum Schumacher, 1817: 177–179. Type species: *Umbraculum chinense* Lamarck, 1801 [= *Umbraculum umbraculum* (Lightfoot, 1786)] by monotypy.

+ *Umbrella* Lamarck, 1819: 339, 343. Type species: *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)], subsequent designation by Children (1823a).

+ *Gastroplax* Blainville, 1819: 182. Type species: *Gastroplax tuberculosus* Blainville, 1820 [= *Umbraculum umbraculum* (Lightfoot, 1786)] subsequent monotypy by Blainville (1820).

+ *Ombrella* Férussac, 1822: xxx. Type species: *Ombrella indica* Lamarck, 1819) [= *Umbraculum umbraculum* (Lightfoot, 1786)], subsequent designation by O'Donoghue (1929).

+ *Umbella* Delle Chiaje, 1822–1831 [1831]: 200, 209, 213. Type species: *Umbella mediterranea* Lamarck, 1819, by monotypy [ex Valdés (2001)] (= *Umbraculum umbraculum* (Lightfoot, 1786)).

+ *Operculatum* Mörch, 1852: 137. Type species: *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)], subsequent designation by Valdés (2001).

TYLODINA AND *OXYNOE*

Though unable to consult a complete copy of Rafinesque (1814), Valdés (2001) claimed, quite correctly, that "*Tylodina* was originally and validly introduced by Rafinesque in 1814." The title of "Num. XII" of Rafinesque (1814) [we have had access to the copy in the library of the Academy of Natural Sciences of Philadelphia], includes the date "1 Dicembre 1814." Only pages 161 and

162 of that work deal with Mollusca, including descriptions of five new genera. Three of them, *Blephalium*, *Opiptera* and *Dicladus*, have disappeared from molluscan literature, but two others, *Tylodina* and *Oxynoe*, are in everyday use. The work is so scarce, only a few copies not being lost with the rest of Rafinesque's possessions in a series of shipwrecks, and the wording so significant, we feel it is essential to repeat verbatim the original descriptions of these two genera here. The original descriptions, in Italian, read: [page 162]

> IV. G. OXYNOE. Corpo repente, con una grande conchiglia dorsale esterna bulliforme, spira semplice, ventre stretto colle branchie intorno e striate, mantello allargato in due ale, due tentacoli sporgenti e fissi. Differisce dal g. *Sigaretus* per la sua conchiglia esterna, tentacoli sporgenti + e. 1 sp. *O. olivacea*.

> V. G. TYLODINA. Corpo repente con una piccolo conchiglia esterna sopra il dorso, membranosa, senti spira, ovale, e colla punta callosa, quattro tentacoli i due posteriori allontanati e più grandi branchie sotto la conchiglia al suo lato destra, ano al lato destra del collo. Differische dal g. *Limax* perchè hà una conchiglia esterna e dal g. *Helix* perchè non hà spira. 1 sp. *T. punctulata*

These descriptions were reproduced, in French, by Rafinesque (1819), whose paper is better known from its inclusion in the Binney and Tryon (1864) reprint of Rafinesque's conchological writings. The French descriptions are an exact translation of this earlier (1814) Italian text, extended only by brief notes on each species, and reduced by shortening the comparison for *Oxynoe*, and by removing the comparisons with *Limax* and *Helix* altogether from *Tylodina*.

The description of *Tylodina* is remarkably extensive, and accompanied, however improbable it may seem to present-day opisthobranch workers, by a generic comparison. A single species, *T. punctulata*, is denominated though not described. This combined description meets the requirements of the present International Code of Zoological Nomenclature (ICZN 1999, Article 12.2.6), by which both genus and species are to be attributed to Rafinesque, 1814. *Tylodina punctulata* Rafinesque, 1814, is thus the type species by monotypy of *Tylodina* Rafinesque, 1814. The family name Tylodinidae was published by Gray (1847), who wrote it Tylodinana. The early history of this name, including its brief placement in the Pyramidellidae by Gray (1853), is summarised by Bertsch (1980).

An exactly similar situation occurs with *Oxynoe*, with original combined description of a new nominal genus and single new nominal species. Thus *O. olivacea* Rafinesque, 1814 is the type species by monotypy of *Oxynoe* Rafinesque, 1814. The earliest use of a family name based upon this genus appears to be Oxynoeidae Stoliczka, 1868, correctly written these days as Oxynoidae.

Fischer-Piette (1943) examined and figured the actual specimen upon which Adanson (1757) based his "Le Liri" from Senegal, and which Gmelin (1791) formally named *Patella perversa*. Fischer-Piette (1943) transferred *P. perversa* to *Tylodina*, declaring it the senior synonym of *T. citrina* Joannis, 1853, the name then in use for this Mediterranean species. Since that date (i.e., 1943), the name *Tylodina perversa* has been used exclusively. In his description of the animal of "Le Liri", Adanson (1757) was impressed by the fact that the body projected forward from the end of the shell further from the apex, whereas in the patelliform species described in great detail on the preceding pages, the head was at the end closer to the apex. He commented upon this relationship between shell apex and head of animal as "mais dans un sens contraire." This undoubtedly explains Gmelin's choice of *perversa* [Latin: turned wrong way round] for the name of this species.

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Ángel Valdés's paper (2001) provoked one of us (RB) to commit to paper nomenclatural information gathered slowly over more than forty years of amateur opisthobranch enthusiasm. Malacologists, museums and libraries in Australia, Europe and North America graciously provided access to their resources or copies of pertinent works. The Academy of Natural Sciences of Philadelphia serendipitously revealed to us the elusive 12th part of Rafinesque's *Specchio* (1814). To each and all, we give grateful thanks.

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Book Review

Invertebrate Zoology: The Mideastern Invertebrate Fauna. Part II: The Coelomates.

Soliman, G. N. 2001. Invertebrate Zoology. The Mideastern Invertebrate Fauna. Part II: The Coelomates. The Palm Press, Cairo, Egypt. 520 pp., 8 color plates.

This is the second volume of Dr. Gamil Soliman's work on the invertebrate fauna of the Middle East, including Egypt. This volume covers 17 phyla with major sections devoted to the Mollusca and the Arthropoda. Volume 2 devotes 140 pages in 4 chapters to the mollusks and 176 pages in 4 chapters to the Arthropoda, the two largest phyla of animals. The examples and illustrated animals are drawn for those native to the Middle East. The taxonomy used in this volume is a synthesis of all information available. Each phylum is introduced in a short description, followed by a summary of the higher classification within the phylum, anatomy, respiration, nervous system, reproduction, a summary, key terms, ending with a discussion of the phylogeny of the phylum. The sections vary in length due to the amount of knowledge available on each phylum or class. The text also includes boxes, expanding on topics of special interest, e.g., types of gastropod radulae, gastropod egg masses, pearl formation, bivalve hinge types, growth and molting in arthropods, and comparison of Protostomia and Deuterostomia. The excellent text figures are complimented by eight plates of color photographs of representative animals of the phyla covered in this volume.

Dr. Soliman worked on these two volumes at the Academy of Natural Sciences of Philadelphia part of each year since 1981. During his yearly visits, he worked completing his research and writing the text of these two volumes as well as drafting the numerous excellent illustrations. It was my great pleasure and inspiration to watch as the numerous figures took shape, to see the text filled out and the two volumes come together. I had the pleasure of reading drafts of most of the chapters. I am pleased to see the finished volume. This work is not just your average university level invertebrate zoology textbook. Soliman's volume represents a summation of his life work. He is a malacologist by training, as well as an accomplished artist. This can be seen in the expanded treatment of the Mollusca in this second volume. The attention to detail and anatomy clearly shows his love of this group. He has chosen as the representative for the Bivalvia, *Spathopsis rubens* (Unionoida: Iridinidae), to be discussed in detail. This is the most comprehensive published treatment of the anatomy of a species of the family Iridinidae of Africa. He similarly uses *Sepia savignyi* as the representative of the Cephalopoda to illustrate the anatomy and reproduction of this class of Mollusca.

This textbook will be a great aid to the teaching of invertebrate zoology and also will also serve as a major resource volume. I especially like, in addition to the overview of the classification and detailed anatomy, the summary section in numbered bullet format and the listing of key terms. These sections are important for any student of invertebrates. The section on phylogeny pulls together the latest morphological and genetic data on the relationships within and between phyla. I would recommend that this volume along with its companion volume should be on the bookshelves of all invertebrate biologists.

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Notice

THE 2003 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2003 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable mollusk systematists to visit the museum for a period of one week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1580
Sanibel, FL 33957
jleal@shellmuseum.org

Applications for the 2003 Visiting Curatorship should be sent no later than May 30, 2003. The award will be announced by late June. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

(239) 395-2233; fax (239) 395-6706.

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Science Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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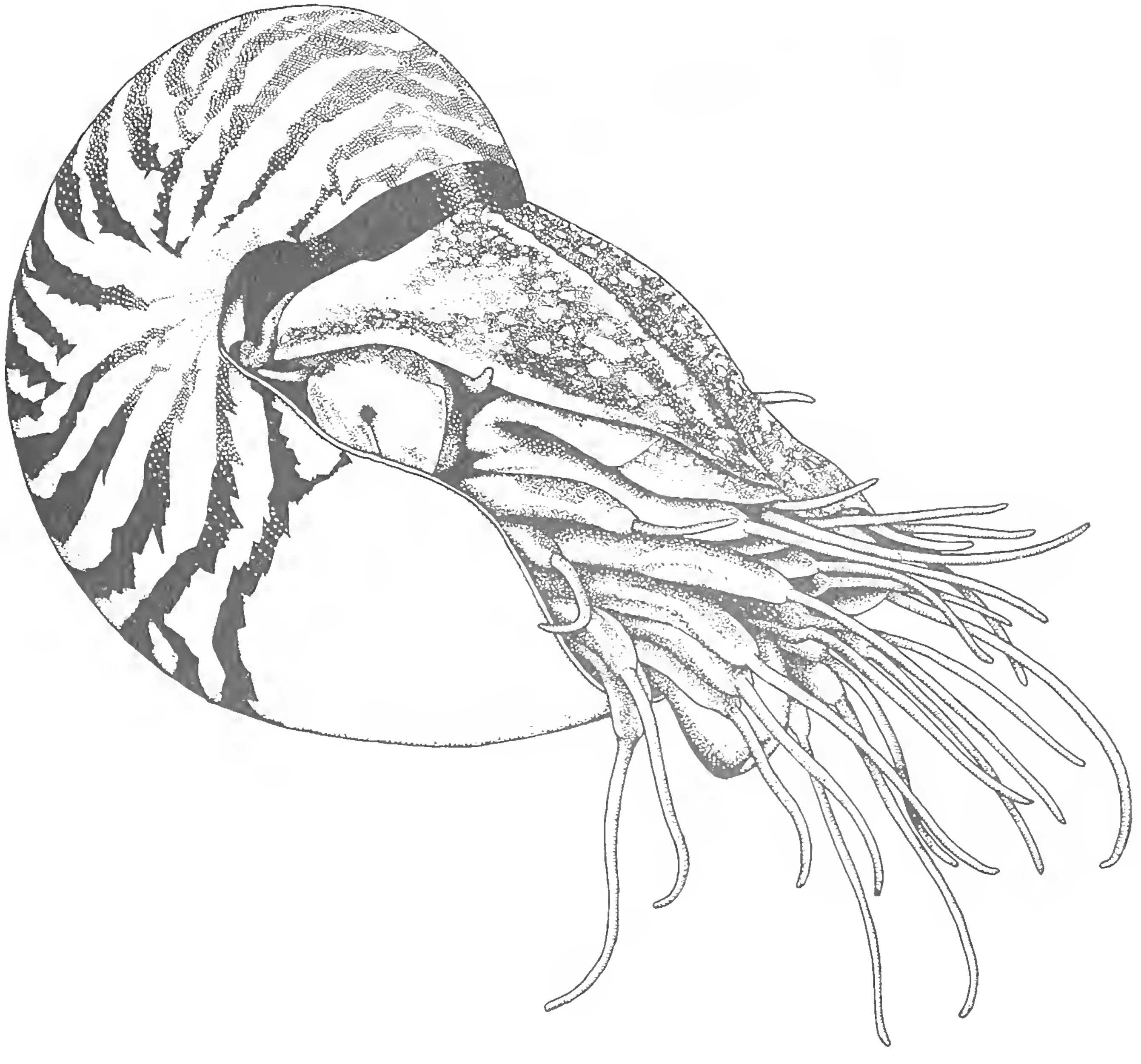

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CONTENTS

Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus

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ABSTRACT

Two new species and a new genus of large mussels from off northern New Zealand are described: *Bathymodiolus tangaroa* new species from seeps (presumably methane-rich) off Cape Turnagain and Cape Kidnappers at 920–1205 m, and *Gigantidas gladius* new genus and new species from active submarine volcanoes on the southern Kermadec Ridge at 216–755 m. *Gigantidas gladius* is anatomically closer to the small, wood-associated species of *Idas* Jeffreys, 1876, than to any of the large mussels currently known from hydrothermal vents or seeps. A polychaete of the genus *Branchipolynoe* Pettibone, 1984 was found within the mantle cavity of every specimen of *Gigantidas gladius*.

INTRODUCTION

Following the discovery of a number of species of large mussels associated with seeps and hydrothermal vents from the eastern Pacific, Japan, Fiji, the Caribbean, the Gulf of Mexico, and the Mid-Atlantic Ridge (Kenk and Wilson, 1985; Cosel et al., 1994; Hashimoto and Okutani, 1994; and references therein), examples of a related species were obtained by commercial fishing at two sites off the east coast of the North Island of New Zealand (Lewis and Marshall, 1996) (Figure 18). This mussel, here referred to as the genus *Bathymodiolus* Kenk and Wilson, 1985, occurs on slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate.

A second, much larger species was obtained subsequently by dredging during surveys of active submarine volcanoes present along the southern Kermadec Arc off northeastern North Island (Parson and Wright, 1996; Wright, 1994, 1997; de Ronde et al., 2001; and references therein) by the National Institute of Water and Atmospheric Research, Wellington (Figure 42).

Institutional abbreviations used in the text are: MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; NIWA, National Institute of Water and Atmospheric Research, Wellington.

SYSTEMATICS

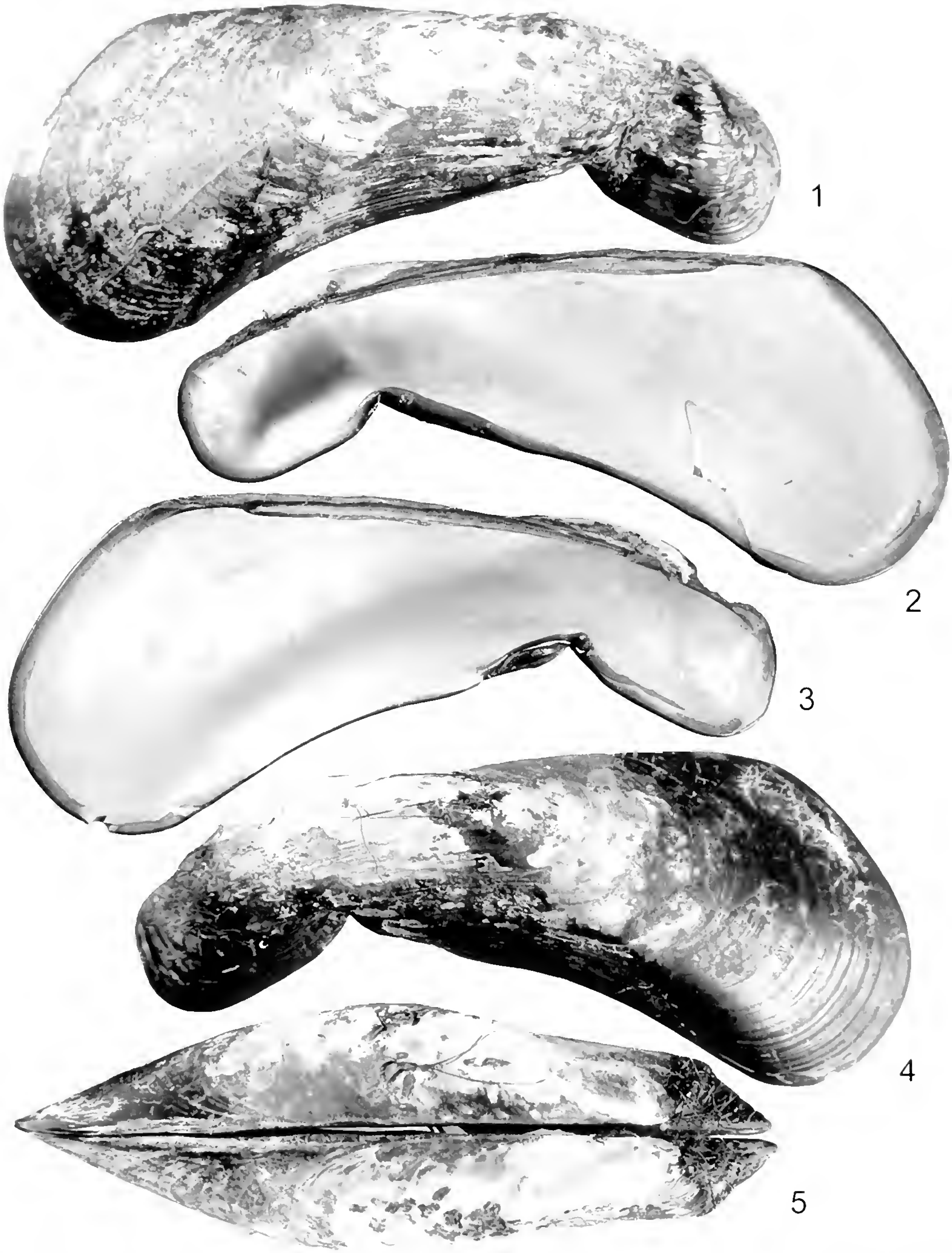
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Genus *Bathymodiolus* Kenk and Wilson, 1985

Bathymodiolus Kenk and Wilson, 1985: 255. Type species (by original designation): *Bathymodiolus thermophilus* Kenk and Wilson, 1985; Recent, Galapagos Rift.

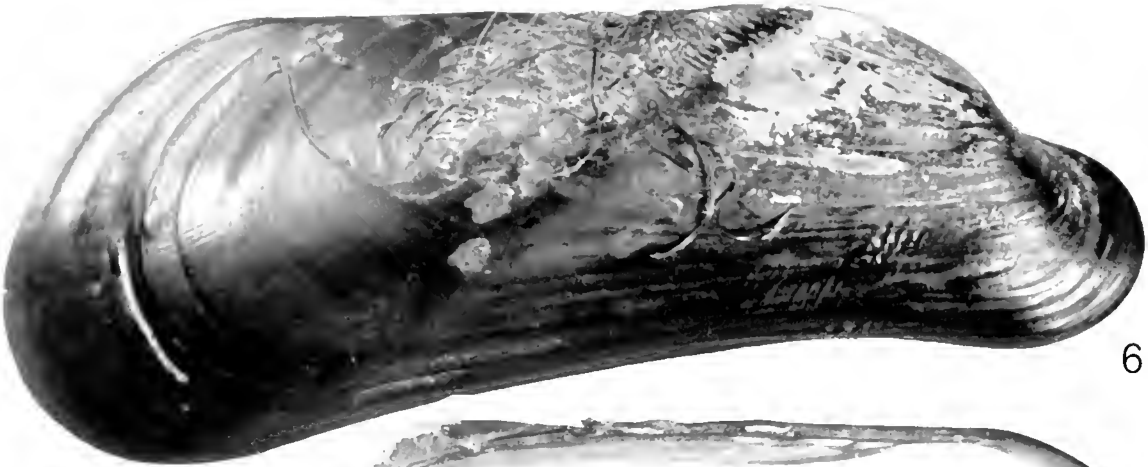
Bathymodiolus tangaroa new species
(Figures 1–13, 15–18, Table 1)

aff. *Bathymodiolus* sp.—Lewis and Marshall, 1996: 183; 186, fig. 4; 187.
Bathymodiolus sp.—Cosel and Olu, 1998: 658.
Bathymodiolus sp. H—Cosel, 2002: table 4.

Description: Shell large, up to almost 200 mm long, elongate, somewhat aduliform, rather thick and solid, externally with well-developed, irregular growth lines; dull-whitish beneath periostracum; internally nacreous-ivory. Beaks subterminal, at about one-seventh total shell length in adults; umbones very broad, flattened. Height gradually increasing posteriorly, markedly curved dorso-ventrally, most inflated at about mid-length, equivalve, length/height ratio 2.5–3.2. Few specimens somewhat twisted. Anterior part short, rather narrow, protruding nose-like anteriorly; anterior margin narrowly but evenly rounded; ventral margin markedly concave over anterior half. Posterior margin evenly rounded ventrally, convex dorsally; postero-dorsal angulation well-defined, rounded, situated above posterior adductor scar, close to posterior margin. Prodissoconch unknown. Periostracum thick, hard, dark brown, smooth, glossy to somewhat dull, no periostracal hairs (byssal endplates of other specimens scattered over valves). Hinge (adults) toothless, anterior hinge margin weakly protruding ventrally. Ligament opisthodetic, very strong, extending over



Figures 1–5. *Bathymodiolus tangaroa* new species. Holotype, Madden Basin, shell length 199.6 mm, NMNZ M.158284. **1, 2.** Exterior and interior of right valve. **3, 4.** Interior and exterior of left valve. **5.** Dorsal view.



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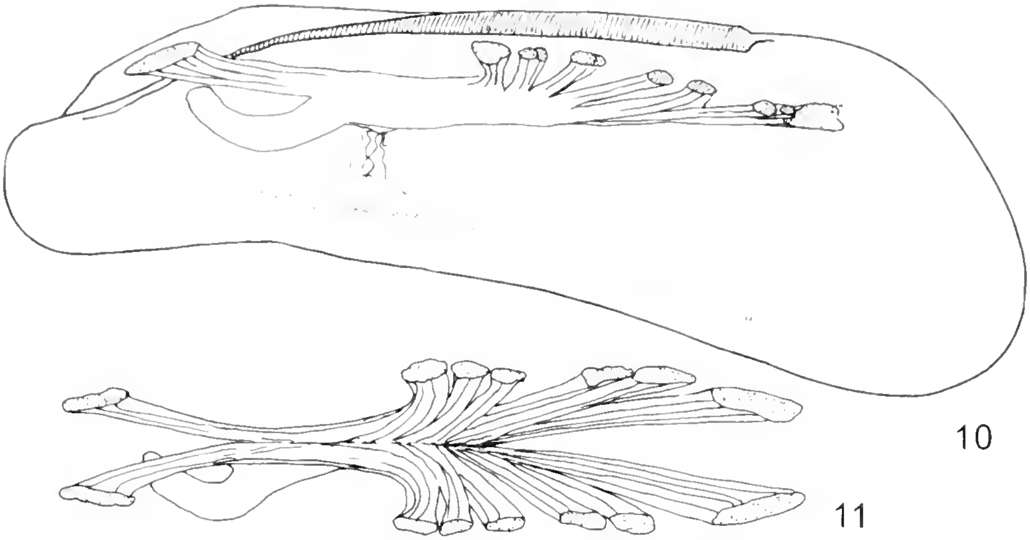
Figures 6–9. *Bathymodiolus tangaroa* new species. **6, 7.** Paratype 8, Madden Basin (shell length 110.5 mm, NMNZ M.158227/8). Exterior and interior of right valve. **8, 9.** Paratype 3, Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). Lateral and oblique ventral view of interior of right valve, with muscle scars and pallial line highlighted.



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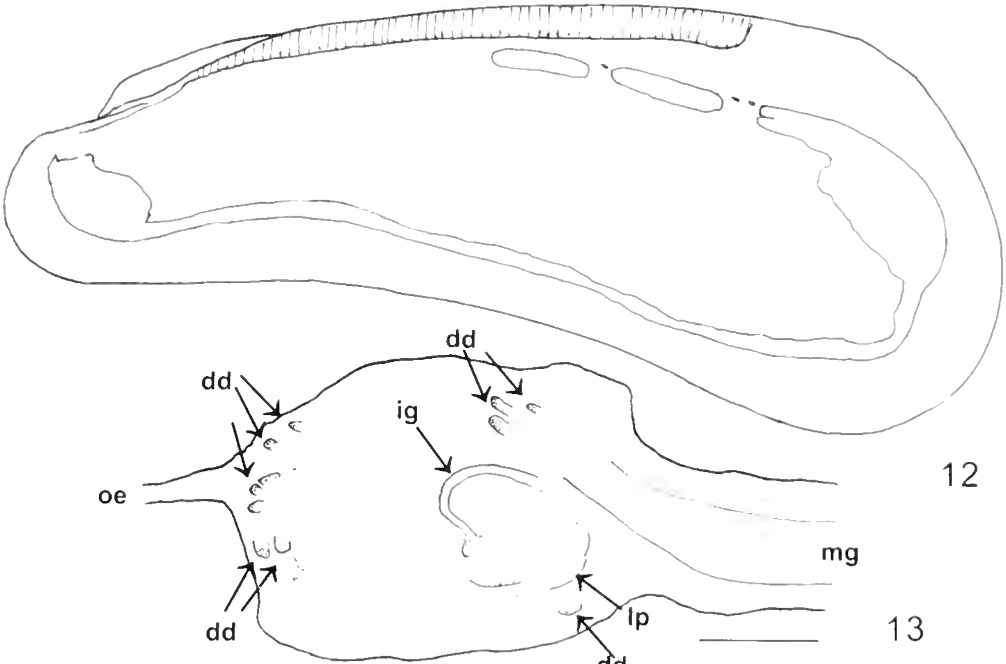

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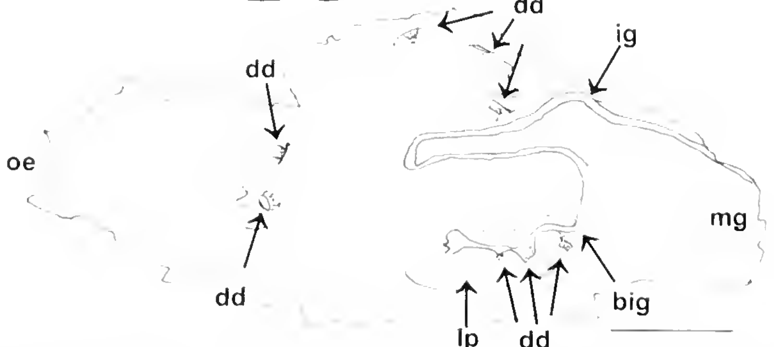

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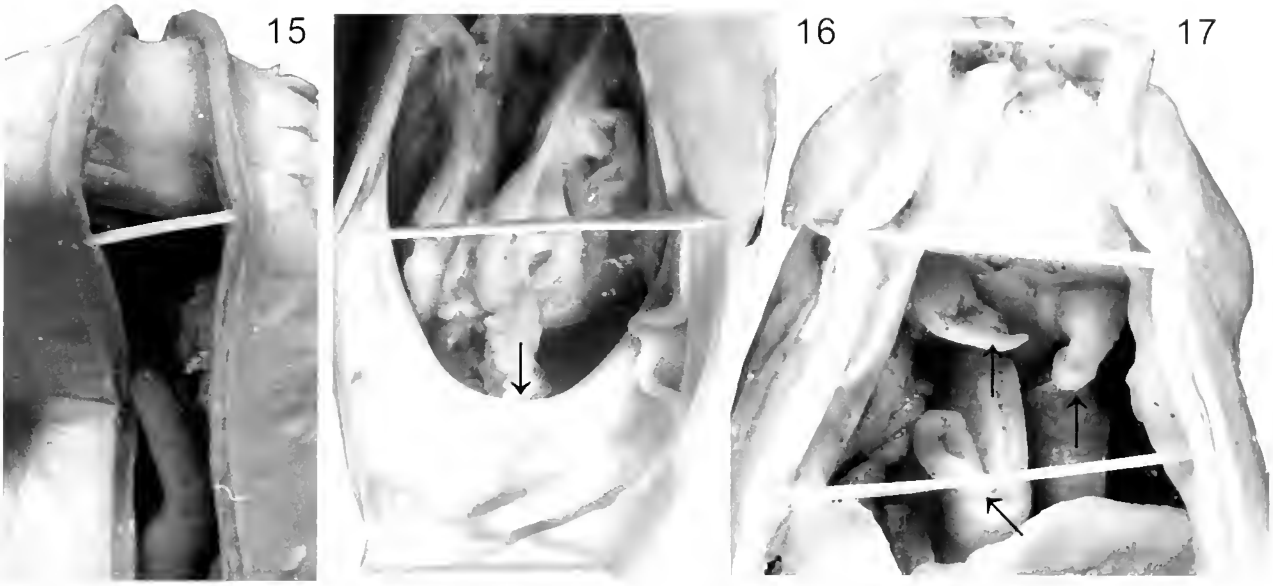
Figures 10–11. *Bathymodiolus tangaroa* new species and *Gigantidas gladius* new species, half schematic drawings. **10, 11.** *Bathymodiolus tangaroa* paratype 3, off Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). **10.** Sketches of foot-byssus retractor complex in left lateral (10) and dorsal (11) view and its situation in the shell. **12.** *Bathymodiolus tangaroa* paratype 5, off Cape Kidnappers (shell length 161.5 mm, MNHN). Interior of right valve, showing muscle scars and pallial line. **13.** *Bathymodiolus tangaroa* paratype 1, Madden Basin (shell length 177.9 mm, NMNZ M.158227/8). Dorsally opened stomach (scale bar = 5 mm). **14.** *Gigantidas gladius* paratype 3, Rumble V (shell length 271.3 mm, NMNZ M.154988/3). Dorsally opened stomach (scale bar = 5 mm). big, beginning of intestinal groove; dd, digestive diverticula duct (entrance); ig, intestinal groove; lp, left pouch; oe, esophagus.



Figures 15–17. *Bathymodiolus tangaroa* new species. **15, 16.** Paratype 3, Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). **15.** Ventral view of anterior end, showing thin, transverse part of inner mantle fold, and ventrally grooved foot. **16.** Ventral view of posterior end, showing valvular siphonal membrane (arrow) without median papilla. **17.** Paratype 6, Cape Kidnappers (shell length 160 mm, NMNZ M.117890/6). Ventral view of anterior end, showing labial palps (arrows).

about five-sixths of postero-dorsal margin in front of postero-dorsal corner, and ending abruptly posteriorly; ligament plate weakly to strongly convex. Subligamental shell ridge well developed, in some specimens divided into a secondary ridge that extends from under umbo for about a third of ligament length; primary ridge extending posteriorly behind umbo, between ligament and secondary ridge, and becoming obsolete shortly before posterior end of ligament (visible only from ventral perspective). Adductor scars well defined. Anterior adductor scar short, situated just in front of umbo. Posterior adductor scar rather large, more or less rounded, united with most posterior scar of posterior pedal and byssus retractor muscle complex; anterior scar of this complex well separated, very long and itself divided into isolated impressions, extending posteriorly from under middle of ligament. Anterior byssus retractor muscle scar situated deep under beak on anterior part of umbonal cavity (visible only from ventral perspective). Pallial line curving parallel to ventral margin.

Anatomy: Ctenidia long, narrow, about 75% of shell length (125 mm long and 13 mm wide in 167 mm specimen), outer and inner demibranchs of equal length, filaments broad and fleshy, food-groove not detected (probably because of poor fixation). Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance, those of inner demibranch fused to visceral mass. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, nor connection bars between free edges and gill axes. Inner mantle folds separate along entire ventral margin length from anterior adductor to posterior margin; edges slightly frilled over most of length, more undulate along posterior 30–50 mm; terminating anteriorly over anterior adductor, folded back directly onto muscle and continuing over it as a thin, delicate, inconspicuous membrane. Valvular siphonal membrane short and thin, without median papilla. Foot-byssus retractor muscle complex moderately elongate; anterior retractor rather short, very broad, inserted in anterior part of long umbonal cavity, most anterior point under beaks (larval shell). Posterior byssus retractor comprising several diverging muscle bundles with common base at base of byssus; anterior part comprising 3 bundles attached to very long scar at about middle of valves, at about a right angle (most anterior bundle) and about 80 and 60° to longitudinal shell axis (second and third bundle); posterior part consisting of 4–5 bundles passing towards 2 attachment points, most posterior bundle just before posterior adductor. Posterior foot retractor long and thin, arising from anterior side of base of foot behind base of anterior retractor muscles, passing parallel to longitudinal shell axis towards anterior bundle of posterior byssus retractor, then bent dorsally to attachment point, where closely appressed to anterior bundle of posterior byssus retractor. Foot relatively small, 35 mm long (byssal orifice included) in a specimen of 167 mm shell length. Two pairs of labial palps present, anterior pair relatively small, posterior pair long and narrowly triangular (respectively 7 mm and 12–13 mm long in a 160 mm specimen). Intestinal tract narrow. Stomach situated just behind middle of anterior half of shell length, simple, thin-walled, anterior chamber ill-defined, posterior chamber longer. Diverticular entrances 13, 7 in anterior chamber, and 6 in posterior chamber. Depression on posterior left side corresponds to left pouch. Midgut

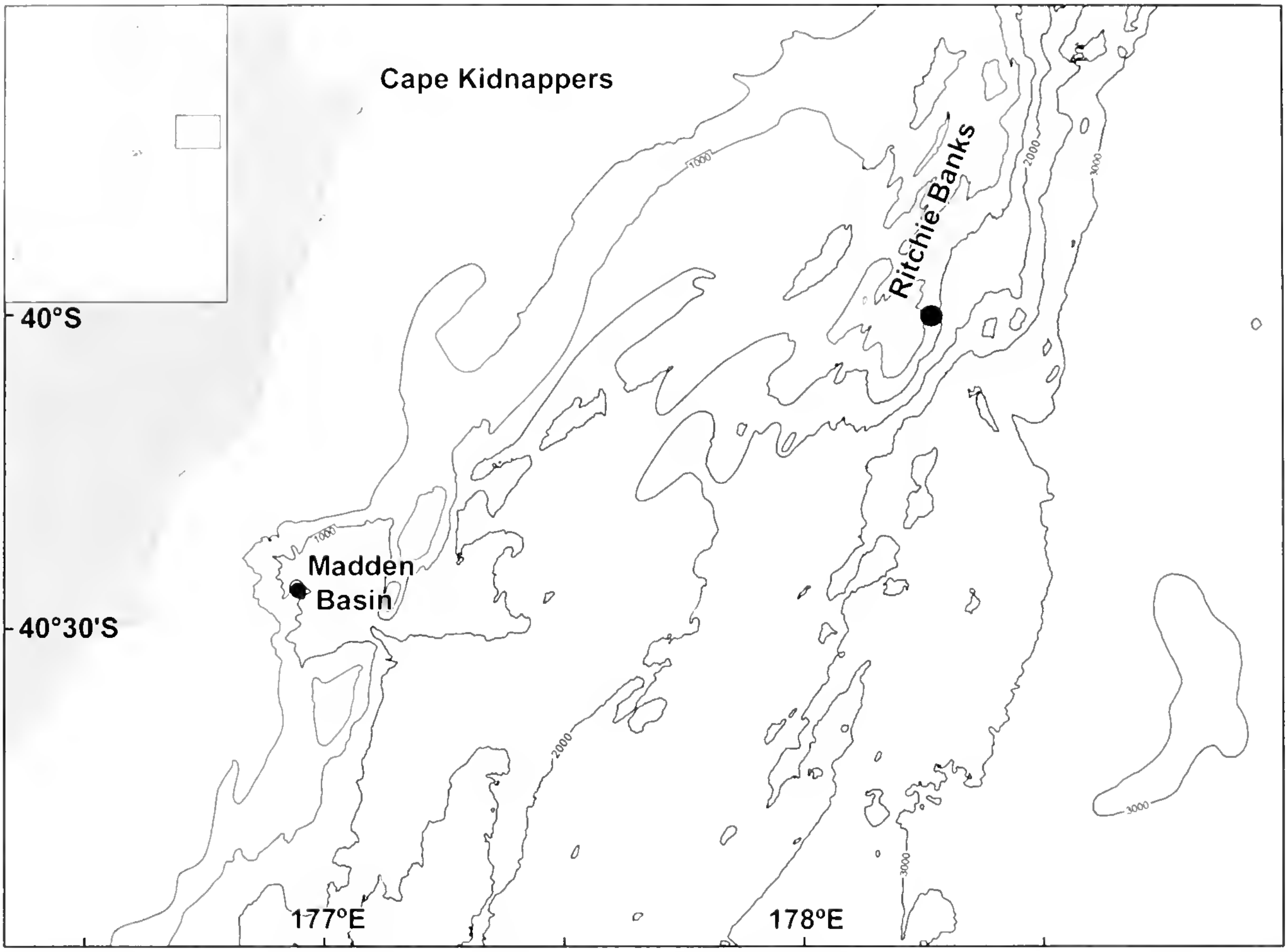


Figure 18. Bathymetric chart of eastern central North Island showing localities for *Bathymodiolus tangaroa* new species. Isobaths at 1000 m intervals, seafloor shallower than 1000 m shaded. Base map courtesy NIWA (adapted).

running posteriorly straight and medially from the stomach, under ventricle and entering ventricle just in front of ostia, without any loop or curve; behind heart, intestine passing over posterior adductor and ventrally on its posterior side; anus at mid-diameter of posterior adductor. Heart rather broad, situated in the posterior half of shell length, anterior extremity of ventricle at mid-shell mantle length. Auricles long, fused posteriorly just in front of the posterior adductor, and stretching out forward in narrow lobes to the anterior bundle of the posterior retractor.

Table 1. *Bathymodiolus tangaroa* new species. Shell measurements (mm) and proportions. Paratypes 3, 5, and 6 from off Cape Kidnappers, others from type locality.

Length	Height	Tumidity	Length/height	Specimen
199.6	71.1	61.2	2.69	Holotype NMNZ
177.9	58.6	50.6	3.03	Paratype 1 MNHN
171.0	58.0	52.5	2.95	Paratype 2 NMNZ
167.8	52.6	53.6	3.19	Paratype 3 NMNZ
162.0	62.0	49.0	2.61	Paratype 4 NMNZ
161.3	63.6	50.7	2.54	Paratype 5 MNHN
160.0	56.6	52.0	2.83	Paratype 6 NMNZ
148.5	53.8	45.5	2.76	Paratype 7 NMNZ
110.5	41.6	37.5	2.66	Paratype 8 NMNZ
103.0	38.6	34.7	2.67	Paratype 9 NMNZ
101.7	40.5	36.8	2.51	Paratype 10 NMNZ

Type Material: Holotype (pair) NMNZ M.158284, and 8 paratypes (6 pairs NMNZ M.158227, 1 pair NIWA P1291, 1 pair MNHN); from type locality, alive, 26 May 2001, FV TASMAN VIKING (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), presented by S. Donker. Paratypes: South Ritchie Bank, SE of Cape Kidnappers, North Island, New Zealand, 40°00.8′ S, 178°16.0′ E, alive, 1170 m, 1994, FV SAN MANUKAU (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), leg. M. Friar (paratypes 3 and 6, pairs, NMNZ M.117890; paratype 5, pair, MNHN).

Type Locality (Figure 18): South side of Madden Basin, off Cape Turnagain, eastern coast of North Island, New Zealand, 40°26.49′ S, 176°58.13′ E, 920–1205 m.

Distribution (Figure 18): Off southeastern North Island, New Zealand, living at 920–1205 m.

Biotope: On hard bottom on the slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate, where plumes of sonar-reflective water, presumably rich in hydrocarbons, rise from the seabed (for details, see Lewis and Marshall, 1996) (Figure 18). We presume that the mussels live at these emission sites and are nourished by methane-metabolizing symbiotic bacteria concentrated in their enlarged gills (Childress et al., 1986; Fisher et al., 1987; Tunnicliffe, 1991; Rio et al., 1992; and references therein).

Etymology: Named after the Maori sea god *Tangaroa*.

Remarks: *Bathymodiolus tangaroa* is strongly characterized by its markedly curved shell and distinctively elongate-cuneiform outline; no other species has this shape. *Bathymodiolus heckerae* Gustafson et al., 1998, from the Gulf of Mexico, is of similar size range but more slender and less curved, with thinner-walled valves. *Bathymodiolus boomerang* Cosel and Olu, 1998, from the Barbados Accretionary Prism, is thinner-walled, more elongate, and considerably larger. *Bathymodiolus brevior* Cosel et al., 1994 (Lau Basin and North Fiji Basin), *B. puteoserpentis* Cosel et al., 1994 (Mid-Atlantic Ridge), and *B. marisindicus* Hashimoto, 2001 (Rodriguez Triple Junction), are shorter and stouter than *B. tangaroa*, with a markedly broader anterior margin. *Bathymodiolus childressi* Gustafson et al., 1998 from the Gulf of Mexico has the cuneiform shape of *B. tangaroa*, but is much shorter with almost terminal umbones.

Bathymodiolus tangaroa differs from *Bathymodiolus* species for which anatomy is known in that the inner mantle fold is much thinner, more delicate, and less conspicuous where it extends transversally over the anterior adductor. *Bathymodiolus tangaroa* differs further from all species other than the group comprising *B. childressi*, *B. platifrons* Hashimoto and Okutani, 1994, *B. mauritanicus* Cosel, 2002, and an undescribed species from Barbados (currently under study by R. v. C.), by its multi-bundle foot-byssus-retractor complex. The posterior retractor in *B. tangaroa*, however, is much longer than the anterior one, rather than *vice versa* as in *B. childressi* (see Gustafson et al., 1998: 77, fig. 13) and the undescribed species from Barbados (condition unknown in *B. platifrons* and *B. mauritanicus*). Another common feature of *B. childressi*, the undescribed Barbados species, and *B. tangaroa* is the lack of a papilla in the middle of the posterior of the valvular siphonal membrane. Thus *B. tangaroa* cannot be assigned to any of the four informal subgroups of *Bathymodiolus* defined by Cosel (2002), specifically the *B. thermophilus* group (one species), the *B. brevior* group (five species), the *B. heckerae* group (two species) and the *B. childressi* group (four species).

Of the 11 specimens examined, one (length 177.9 mm, paratype MNHN) contained a polychaete worm of the genus *Branchipolynoe* Pettibone, 1984 (length 32.5 mm), which was situated in the mantle cavity above the byssus.

Gigantidas new genus

Type Species: *Gigantidas gladius* new species; Recent, New Zealand.

Diagnosis: Shells attaining very large size (length up to 316 mm), extremely slender. Umbones at about 20% of total shell length. Juveniles (<5 mm) with periostracal bristles. Animal with very long, rather narrow, fleshy ctenidia. Inner mantle folds entirely separate, terminating anteriorly over anterior adductor, edges frilled along posterior 3/4 of shell length. No valvular siphonal membrane. Inner mantle folds below posterior adductor with a deep cleft between left and right mantle lobes. Foot very small, anterior retractor inserting on shell directly above anterior adductor, well in front of umbonal cavity, both muscles forming a common scar.

Remarks: The large size and biotope of *Gigantidas gladius* invites immediate comparison with large mussels of the genus *Bathymodiolus*, from all of which, however, it differs by the absence of a well-developed valvular siphonal membrane at the posterior end, and the absence of a continuation of the inner mantle fold across the anterior adductor from one valve to the other. Moreover, unlike *Bathymodiolus* species, the attachment point of the anterior retractor is not situated somewhere within the umbonal cavity but well in front of it, on the narrow anterior part of the valves close to the anterodorsal margin. In *Bathymodiolus*, the anterior adductor and retractor muscles are situated close together at their attachment point, especially in species with terminal umbones, but remain well separated through ontogeny (Figure 10, see also Cosel et al., 1999: figs. 12, 13, 22, 59, 60, 61). In *Gigantidas gladius* both muscles are in contact at their insertion point and form a common scar. Very young specimens of *G. gladius* have periostracal bristles on the postero-dorsal part, whereas these have never been recorded from *Bathymodiolus* species at any stage of growth (e.g. Cosel et al., 1994; Hashimoto and Okutani, 1994; Cosel and Olu, 1998; Cosel et al., 1999).

The attachment point of the anterior retractor in very young specimens of *G. gladius* (<5 mm) is in the umbonal cavity as in adult *Bathymodiolus* species, but with increasing shell size it progressively shifts anteriorly from the anterior part of the umbonal cavity to a position under the antero-dorsal margin, remaining very close to the anterior adductor throughout ontogeny. The only other large mussel known in which the anterior retractor scar is situated in front of the umbonal cavity closely adjacent to the anterior adductor scar, is an undescribed species from the Kaikata Seamount, Japan. According to Hashimoto and Horikoshi's (1989) illustration, the retractor scar in the Japanese species is very close to the adductor scar but not in contact with it, and the two bundles of the posterior retractor are well separated. The Japanese species, which may thus belong in *Gigantidas*, is smaller and more strongly curved than *G. gladius*, and was found burrowing in sediment on a dormant submarine volcano.

Anatomically, *G. gladius* most closely resembles the much smaller mussels of the genus *Idas* Jeffreys, 1876 (type species *I. argenteus* Jeffreys, 1876: North Atlantic) (*I. japonica* up to 8.9 mm long), which live at similar depths associated with decaying wood and whale bones, and *Benthomodiolus* Dell, 1987 (type species *B. lignicola* Dell, 1987: New Zealand) (length up to 17.3 mm), which lives on decaying wood. In the absence of animals of the type species of *Idas* for comparison, we have had to base our comparison on specimens of the New Zealand *Idas* species identified by Dell (1987) as *I. japonica* (Habe, 1976) (NMNZ M.75022). This species and *G. gladius* share a similarly-shaped posterior end of the inner mantle fold, with a short, narrow, deep cleft between the left and right mantle lobes, and no valvular siphonal membrane; and lack of tubular prolongation of the exhalent siphon. Periostracal bristles are present in both species, though only in juveniles of *G. gladius*. *Benthomodiolus lignicola* and *G. gladius* both have periostracal bristles, and lack a valvular siphonal membrane, and a tubular prolongation of the exhalent siphon. *Gigantidas* thus differs from *Idas* primarily in the exceptional size and the biotope of the type species, and in the migration of the insertion of the anterior retractor to a position in front of the umbones.

Species of *Adipicola* Dautzenberg, 1927, which attain up to 31.3 mm in length, are also similar in gross facies. Since soft parts of the type species (*Modiolarca pelagica* Woodward, 1854) were not available for study, we used New Zealand species referred there by Dell (1987, 1995), for comparison, notably *A. arcuatilis* Dell, 1995, a species with a slender, curved shell, living on whale bones. In contrast to *G. gladius*, the inner mantle folds of *A. arcuatilis* are much thinner and less frilled, but at the posterior end, especially over the posterior adductor, they are much more broadened to form a long, thin lobe that extends posteriorly below the exhalent siphon. In contrast to the conditions in *I. japonicus* and *G. gladius*, a valvular siphonal membrane is present in *A. arcuatilis*, but reduced to a narrow, transversely very short rim without a papilla. Moreover, *A. arcuatilis* has a long, tubular exhalent siphon and no periostracal bristles at any stage of growth. *Adipicola osseocola* (also associated with whale bones) lacks periostracal bristles too, and has a tubular exhalent siphon, though shorter than in *A. arcuatilis*.

From the sum of similarities and differences, we conclude that there is a close relationship between *Gigantidas*, *Idas*, and *Benthomodiolus*, that *Adipicola* has closer affinities with *Bathymodiolus*, and that all of these genera form a single phylogenetic radiation within the Mytilidae.

Gigantidas gladius new species

(Figures 11, 19–43; Tables 2, 3)

Description: Shell exceptionally large for a mussel, up to 316 mm long, 54 mm high and 56 mm broad, extremely long and slender, rather thin for the size but solid, dull-whitish beneath dark periostracum, interior nacreous-white. Outline somewhat variable, irregular, fully grown specimens elongate-aduliform or bean-shaped, slightly curved dorso-ventrally, most inflated about middle or shortly behind it, equivalve, length/height ratio 4.7–6.2. Half-grown specimens already slender and bean-shaped, very young (length < 60 mm) specimens more or less straight. Beaks in adult specimens at about anterior quarter. Anterior part narrow, strongly protruding anteriorly; anterior margin narrowly rounded, ventral margin straight to very slightly concave over anterior half, middle zone of ventral margin markedly concave, straight posteriorly, and slightly convex in posterior fifth. Posterior margin broadly rounded, postero-dorsal margin weakly convex; postero-dorsal corner broadly rounded or not defined, highest part of the valve situated there. Exterior dull, with well-developed, irregular commarginal growth lines. Rounded, pronounced posterior angulation running from umbones towards ventral part of posterior margin, but becoming obsolete on flattened and broader posterior part situated at about 1/7th of shell length. Similar but much shorter anterior angle from umbo to ventral part of anterior margin. Umbones extremely elongated, rather prominent. Fine radial striae running from beaks to anterior, ventral and postero-ventral margins, visible mostly on ventral part of valves, sometimes slightly changing direction at commarginal growth lines. Radial striae weakly reflected on shell interior, mostly ventrally. On postero-dorsal slope striae replaced by low, broad longitudinal waves that bifurcate towards both dorsal margin and posterior angle (Figure 35). Posterior angle smooth. In dorsal or ventral view, broadest part of shell formed by posterior angle. Second broadest part at anterior angle; section under umbones between anterior and posterior angle about same width as anterior angle, in large specimens even slightly constricted there (Figure 27). In some specimens whole shell often more or less spirally twisted. Ligament plate almost straight to slightly convex. Periostracum strong, dark brown, umbonal region and area under umbones light brown, glossy to somewhat dull, smooth; very young specimens (3–6 mm), however, with short periostracal bristles (byssal endplates of other specimens commonly scattered over surface of valves). Hinge in very young specimens (up to about 5 mm long) with row of small denticles of similar size, extending posteriorly from ligament to postero-dorsal angulation, toothless in larger specimens. Anterior hinge margin hardly protruding towards ventral, if at all. Ligament opisthodetic, strong, extending almost over whole of postero-dorsal margin and ending posteriorly 10–20 mm (specimens 200–270 mm shell length) in front of postero-dorsal corner, either abruptly or in a rather short

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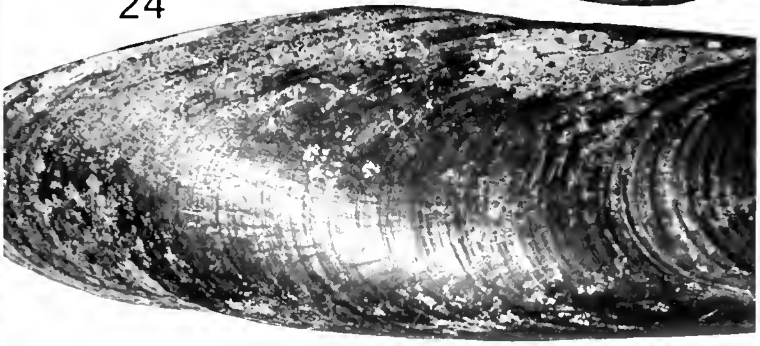

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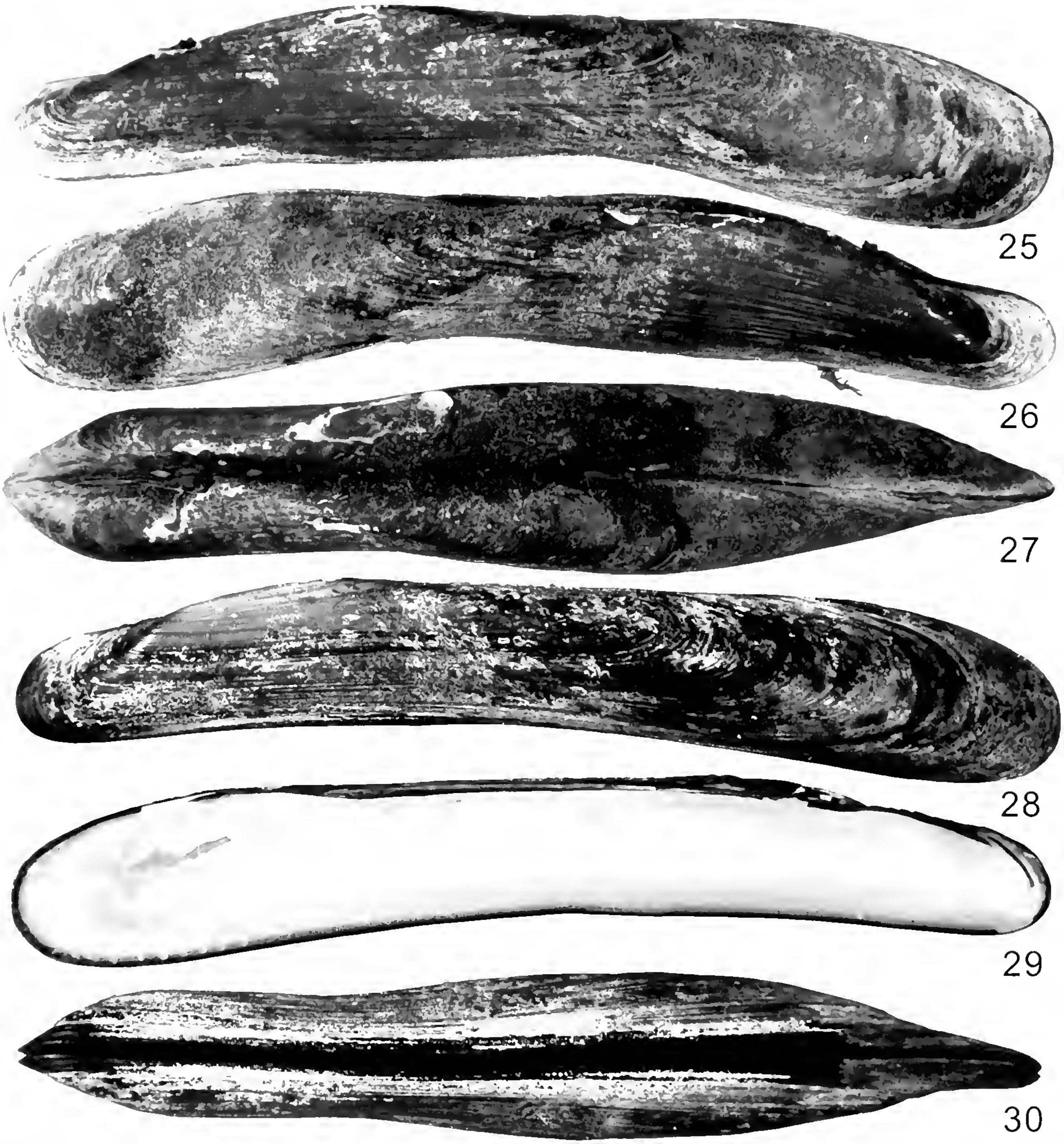
Figures 19–24. *Gigantidas gladius* new species. **19–22, 24.** Holotype, Rumble V (shell length 260 mm, NIWA H 790). **19–21.** Exterior, interior and oblique ventral views of right valve. **22.** Exterior of left valve, muscle scars and pallial line highlighted. **24.** Close-up view of posterior part of right valve to show sculpture. **23.** Prodissoconch of juvenile paratype from Rumble III (NMNZ M 158285). Prodissoconch I and II boundaries arrowed (scale bar = 200 mm).

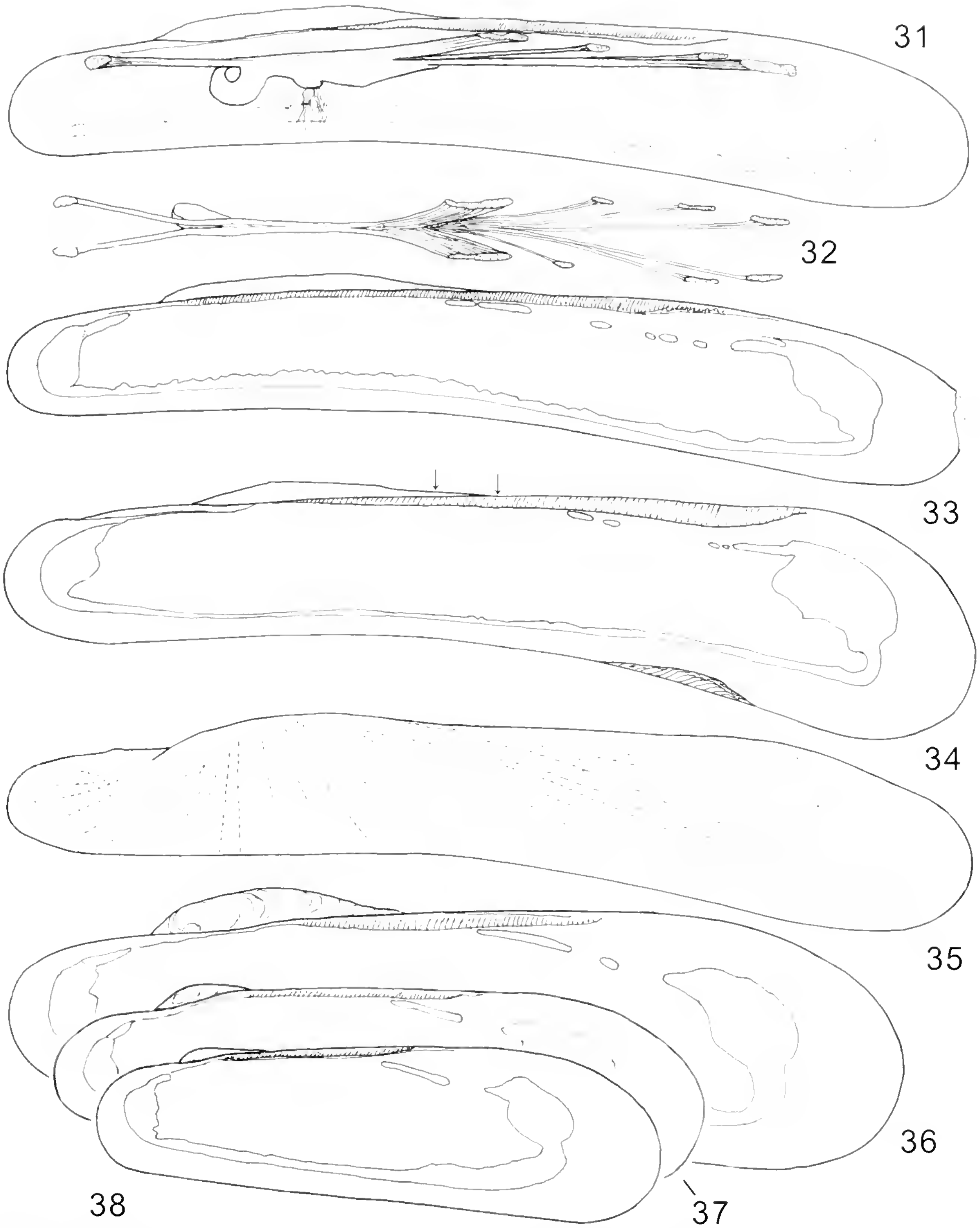
taper. Subligamental shell ridge well developed from under umbones to about one-half of ligament length, then becoming gradually obsolete, visible under the beaks only from ventral perspective. Adductor scars clearly defined. Anterior adductor scar rather large, arched, situated well in front of umbo, near antero-dorsal margin, united with anterior retractor muscle scar. Posterior adductor scar large, rounded to subangular, united with posterior scar of posterior pedal and byssus retractor muscle scar. Anterior scar of posterior retractor well separated, situated between third and last quarter of ligament length. Anterior byssus retractor muscle scar directly above anterior adductor scar and united with it, well in front of umbones. Pallial line almost parallel to ventral margin. Prodissoconch with glossy, ovate, pinkish purple, sharply delineated, prodissoconch I 83–100 µm wide, prodissoconch II 430 µm wide (development planktotrophic).

Anatomy: Ctenidia very long and narrow, length more than 75% of shell length (78% in shell 271 mm long, 84% in 316 mm specimen); 14 mm broad (outer demi-



Figures 25–30. *Gigantidas gladius* new species. **25–27.** Paratype 1 (Rumble III; shell length 316 mm, NMNZ M.154988/1). **25.** Exterior of left valve. **26.** Exterior of right valve. **27.** Dorsal view. **28–30.** Paratype 3 (Rumble V; shell length 271.3 mm, NMNZ M.154988/3). **28, 29.** Exterior and interior of left valve. **30.** Ventral view.

branch; in a 270 mm specimen, outer and inner demibranchs of equal length; filaments broad and fleshy. Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance (about 5 mm), those of inner demibranch fused to visceral mass. Ventral edge of each demibranch with a well-marked food-groove, broader on inner demibranch. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, and no connection bars between free edges and gill axes. Inner mantle folds separate along whole length of ventral margin from anterior adductor to posterior margin, their edges frilled along posterior fifth of shell length or even less, becoming smooth towards anterior, terminating anteriorly over an-



Figures 31–38. *Gigantidas gladius* new species, half-schematic drawings. **31–33.** Paratype 3 (shell length 271.3 mm, NMNZ M.154988/3). **31–32.** Sketches of foot–byssus retractor complex in left lateral (31) and dorsal (32) view and its situation in the shell. **33.** Interior of right valve showing muscle scars and pallial line. **34.** Paratype 11 (shell length 206.5 mm, NMNZ M.154988/11). Interior of right valve showing muscle scars and pallial line; location of concealed anterior bundles arrowed. **35.** Paratype 7 (shell length 245.5 mm, NMNZ M.154988/7). Exterior of left valve showing orientation of fine sculpture. **36–38.** Right valves of juvenile paratypes, Rumble III, lengths 72.8 mm (36), 39.8 mm (37) and 34.7 mm (38) (NMNZ M.158285).

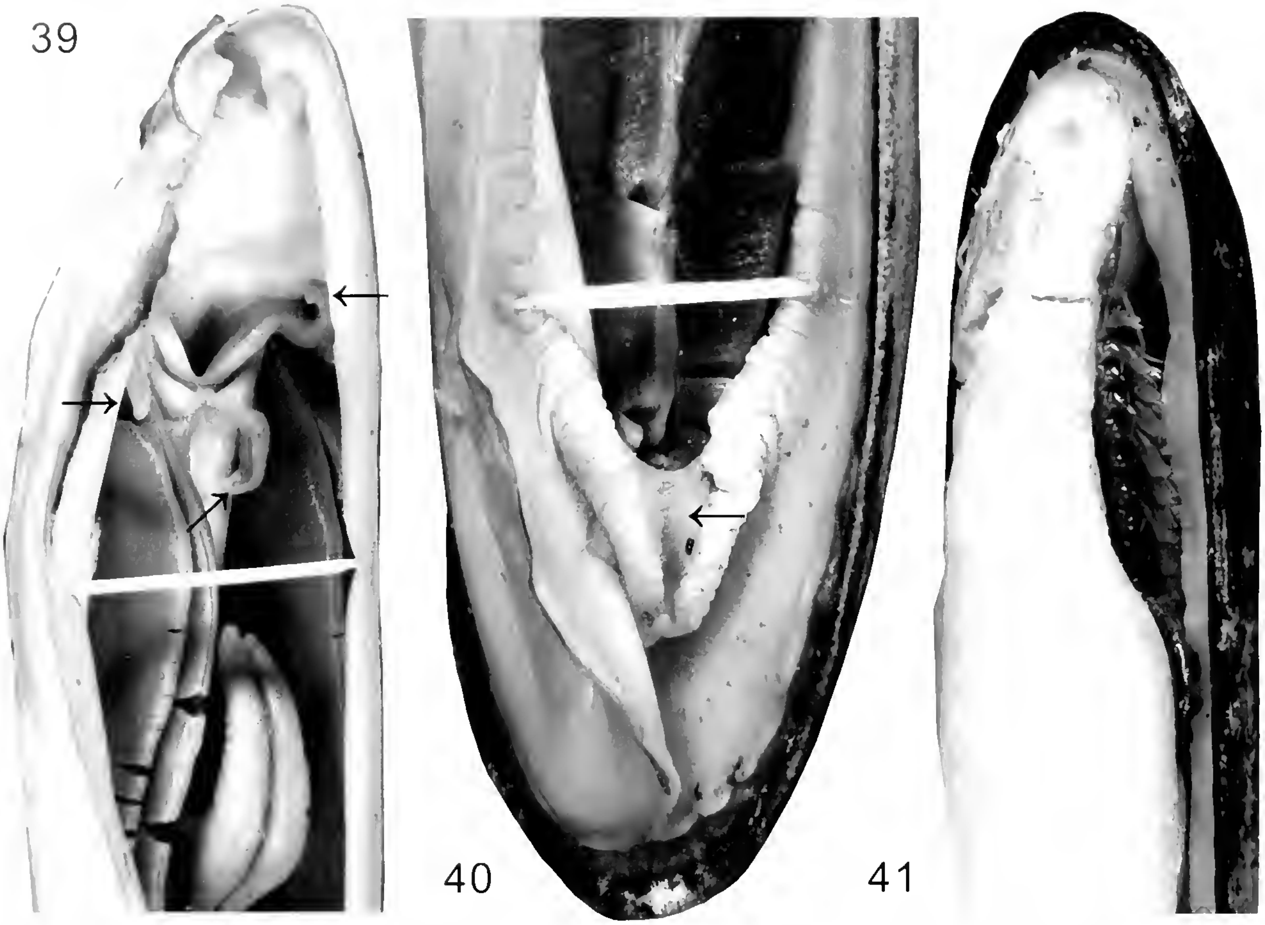


Figure 39–41. *Gigantidas gladius* new species. **39.** Paratype 11, Rumble V (shell length 206.5 mm, NMNZ M.154988/11). Ventral view of anterior end showing mantle edge, anterior and posterior labial palps (arrows), enlarged gills, ventrally-grooved foot, and absence of transverse part of inner mantle fold. **40.** Paratype 9, Rumble V (shell length 231.2 mm, MNHN). Ventral view of posterior end showing muscular connection, cleft posteriorly (arrow) and with vestige of valvular siphonal membrane anteriorly. **41.** Parasitic worm Branchipolynoe sp. (length 34 mm) in situ with associated lesion on anterior mantle edge of paratype 9 of G. gladius (shell length 231.2 mm, MNHN).

terior adductor and folding back directly onto adductor but not continuing transversally over it as a rim to meet mantle fold of opposite side. Valvular siphonal membrane absent; however, inner mantle fold folded ventrally and becoming very strong and strongly frilled, with a deep cleft between those of right and left valve. Foot very small: length 34 mm (byssus orifice included) in a specimen of 270 mm shell length. Foot-byssus retractor muscle complex extremely elongated, but anterior retractor rather short. Anterior retractor in adults inserting immediately above anterior adductor (near antero-dorsal margin) and well in front of umbonal cavity. In very young specimens (< 5 mm long) attachment point is well within anterior part of umbonal cavity though still close to anterior adductor, attachment point migrating anteriorly with increasing size. Posterior byssus retractor comprising 2 principle diverging muscle bundles with common base at base of byssus: anterior bundle broadest, descending at a very low angle to longitudinal shell axis from attachment point at about mid shell length, posterior bundle thinner, extremely long, extending about parallel to longitudinal shell axis to attachment point just in front of posterior adductor. Two additional very thin bundles attached between anterior and posterior bundles; attachment points varying somewhat from specimen to specimen. Posterior foot retractor very long, passing from anterior side of foot base, behind base of anterior retractor muscles, towards anterior bundle of posterior byssus retractor, reaching attachment point closely appressed to bundle for only a very short part of its length. Labial palps irregular, narrow-triangular, very small in adult specimens (anterior palps 2–5 mm long and posterior pair about 8 mm long in a 270 mm specimen), relatively slightly larger in juvenile and half-grown specimens (posterior palps about 3.5 mm long in a 77 mm specimen). Intestinal tract narrow. Stomach situated between first and second quarters of shell length, small in relation to shell size, rather simple, thin-walled, with a small, rather poorly defined anterior chamber; posterior chamber longer and broader; 8 di-

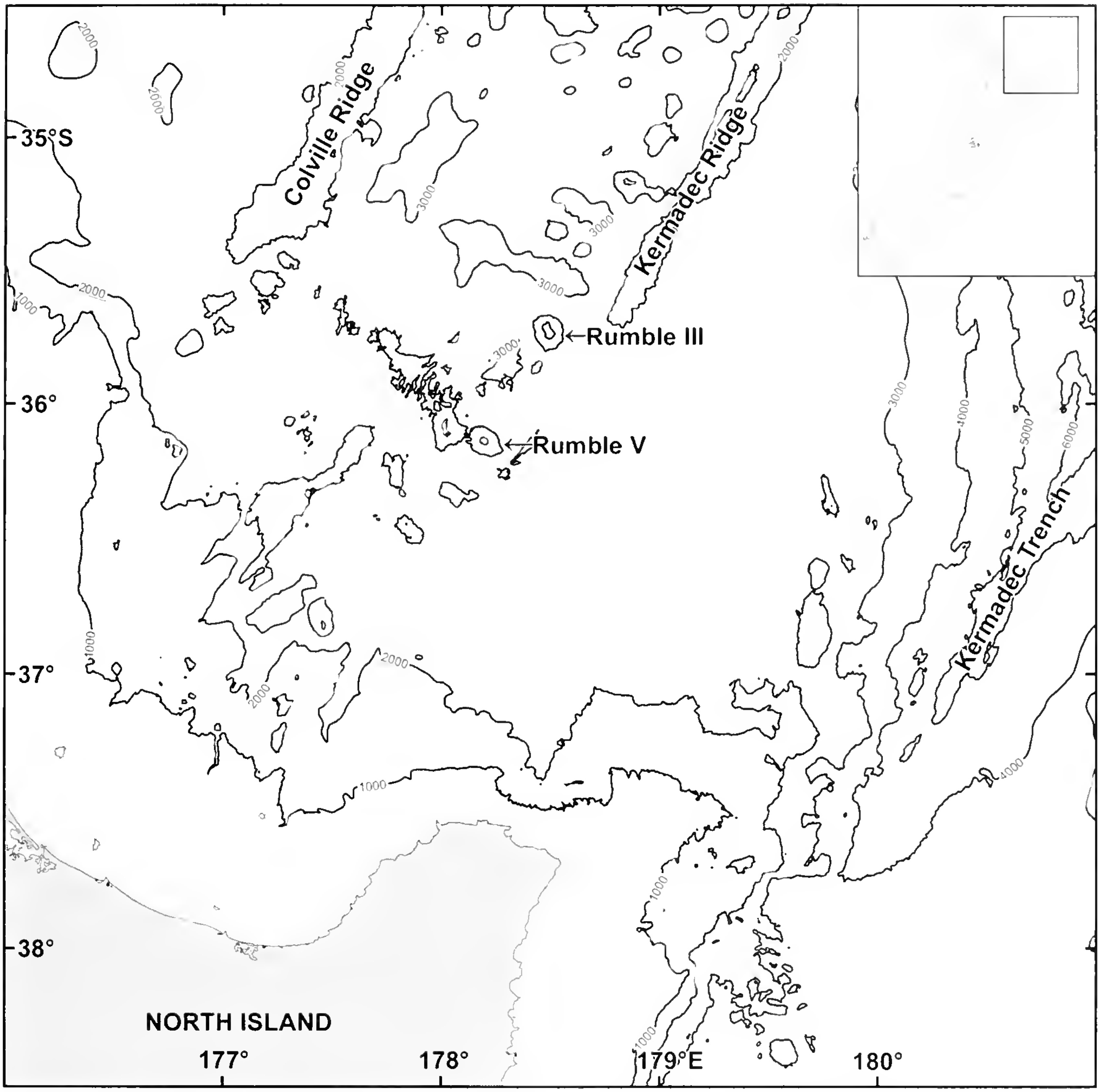


Figure 42. Bathymetric chart showing locations of Rumble III and Rumble V submarine volcanoes, collecting sites for *Gigantidas gladius* new species. Isobaths at 1000 m intervals, seafloor 2000 m and shallower shaded. Base map courtesy NIWA (adapted).

gestive diverticulum entrances visible, 3 at end of anterior chamber, 5 in posterior chamber (specimen examined contained mucus only). Style sac and midgut conjoined. Major typhlosole passing from midgut along floor of posterior chamber to somewhat behind anterior chamber; shallow depression corresponding to left pouch on posterior left side. Gastric shield not detected. Midgut extending posteriorly straight and medially from stomach, passing under ventricle, then turning upwards and entering ventricle without any coiling or loop, passing behind heart over posterior adductor and on posterior side of adductor turning ventrally, anus at mid-diameter of adductor. Heart rather narrow, situated well posteriorly, its long auricles fused posteriorly just in front of posterior adductor, extending anteriorly in long and narrow lobes to midpoint of shell mantle length.

Type Material: Holotype NIWA H.790 (pair, preserved in alcohol) and paratypes NMNZ M.154988 (5), NIWA P.1246 (7), MNHN (2), all from type locality: 24 May 2001, R/V *Tangaroa* (stn 107/230). Paratypes: Rumble III submarine volcano, S Kermadec Ridge, 35°44.47′

Figure 43. *Gigantidas gladius* new species in situ on Rumble III volcano, 386 m, 22 May 2001 (NIWA sta TAN107/152). The largest mussels in the foreground at lower right and at top left centre are 250–300 mm long. The starfish is a new genus and species of the Asteroidae (D.G. McKnight, pers. comm.). From color photograph taken by remote camera (courtesy NIWA).

Table 2. *Gigantidas gladius* new species. Shell measurements (mm) and proportions.

Length	Height	Tumidity	Length/height	Specimen
316.0	54.1	56.1	5.84	Paratype 1 NMNZ
288.0	46.7	43.2	6.17	Paratype 2 MNHN
271.3	44.0	45.3	6.16	Paratype 3 NMNZ (dissected)
270.0	56.6	48.5	4.77	Paratype 4 NMNZ (broken)
260.0	45.0	44.7	5.78	Holotype NIWA
253.5	47.0	44.7	5.39	Paratype 5 NMNZ (Lv broken)
247.8	44.8	40.6	5.53	Paratype 6 NIWA
245.5	43.1	40.2	5.69	Paratype 7 NMNZ
244.3	45.2	44.0	5.40	Paratype 8 NIWA
231.2	42.3	39.2	5.46	Paratype 9 MNHN
216.5	41.0	40.2	5.28	Paratype 10 NIWA
206.5	44.4	39.7	4.65	Paratype 11 NMNZ

S, 178°29.4′ E, alive, 216–460 m, 2 Nov. 2000, R/V Kaharoa (many juveniles; NMNZ M.158285, NIWA P.1248 (KAH11/21), MNHN).

Type Locality: Rumble V submarine volcano, southern Kermadec Ridge off northeastern North Island, New Zealand, 36°08.18′ S, 178°11.70′ E, 755–360 m.

Other Material Examined: Rumble III, 238–350 m, 2 Nov. 2000, R/V Kaharoa (many small to moderate-sized specimens, NIWA P.1249 (KAH11/22); R/V Kaharoa (36 pairs, NIWA P.1250 (KAH11/12); 382–207 m, 19 May 2001, R/V Tangaroa (51 pairs, NIWA TAN107/002); 420–220 m, 19 May 2001, R/V Tangaroa (78 pairs, NIWA TAN107/005); 420–230 m, 23 May 2001, R/V Tangaroa (253 pairs, NIWA TAN107/216); Rumble V, 755–360 m, 24 May 2001, R/V Tangaroa (103 pairs, NIWA TAN107/230); 730–470 m, 24 May 2001, R/V Tangaroa (27 pairs, NIWA TAN107/324); 485–415 m, 24 May 2001, R/V Tangaroa (90 pairs, NIWA P.1247; TAN107/325).

Table 3. Polychaete worms (*Branchipolynoe* sp.) associated with *Gigantidas gladius* new species

Shell length	Worm length	Location of worm within mussel, and pathology
316.0 mm	35 mm	In front of foot between right ctenidium demibranchs
288.0 mm	15 mm	Below posterior adductor
271.0 mm	39 mm	Anterior half with one end at mid-shell length
270.0 mm	30 mm	Ventral side of foot (lesions on ctenidia both sides)
260.0 mm	35 mm	Posterior end. Worm's posterior against posterior adductor
253.5 mm	40 mm	Right side between byssus and ctenidia (lesions on ctenidia both sides)
248.0 mm	34 mm	Between anterior tip of foot and anterior adductor
	9 mm	Beside the adult worm
244.0 mm	37 mm	Hind end at mid-shell length, head posterior
245.5 mm	30 mm	Near mouth, with head touching palps (lesion)
231.0 mm	34 mm	Between tip of foot and anterior adductor (lesion on right mantle edge)
216.5 mm	31 mm	In opening above mouth, about 15 mm of worm projecting posteriorly
206.5 mm	23 mm	Above ctenidia on right side at byssus level

Distribution (Figure 42): Submarine volcanoes, Kermadec Ridge, NE New Zealand, 216–755 m, shallowest occurrence unclear (obtained by dredging upslope), though certainly as shallow as 350 m.

Biotope: High population densities at sulphur-rich hydrothermal springs on active submarine volcanoes (Figure 42). Dredge hauls containing this mussel included elemental sulphur and smelled strongly of it, suggesting that the mussel's nourishment involves chemosynthesis by sulphur-oxidizing symbiotic bacteria concentrated in the extremely enlarged gills.

Etymology: So named because of its blade-shaped valves (Latin).

Remarks: *Gigantidas gladius* is currently the second largest living mytilid known, being only slightly surpassed in length by *Bathymodiolus boomerang* (shell length 316 mm, vs. 370 mm). *Bathymodiolus boomerang*, however, is a true *Bathymodiolus* species with a siphonal membrane and a posterior retractor with only two muscle bundles, and is much higher posteriorly, and more strongly curved anteriorly. Other major distinguishing characteristics of *G. gladius* are the attachment of the anterior retractor well in front of the umbonal cavity directly above the anterior adductor, rather than somewhere within the umbonal cavity as in *Bathymodiolus* species, and the uniting of the anterior adductor and retractor scars, which are separate in *Bathymodiolus* species.

All 11 intact adult type specimens of *G. gladius* contained a polychaete of the genus *Branchipolynoe*. On opening the mussels, the worm was found situated at various sites within the mantle cavity (Table 3), some causing lesions on the mantle edge or in the mouth region. One mussel even had a worm projecting from the opening into the dorsal mantle cavity above the mouth. Thus the mussel is often traumatized by the polychaete (Britayev et al., 2001).

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The tropical eastern Pacific species of the Condylocardiidae (Bivalvia)

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ABSTRACT

There are at least ten minute species of Condylocardiidae in the tropical eastern Pacific: eight species assigned to *Condylocardia* and two to *Carditella*. Eight of these taxa are described here for the first time: *Condylocardia sparsa* new species, *Condylocardia fernandina* new species, *Condylocardia koolsae* new species, *Condylocardia elongata* new species, *Condylocardia kaiserae* new species, *Condylocardia geigeri* new species, *Carditella galapagana* new species, and *Carditella marieta* new species. Many of the new species seem to be endemic to islands.

INTRODUCTION

The Condylocardiidae is a group of minute marine bivalves that brood their young within their mantle cavity. F. Bernard (1897: 205) suggested that they derived by neoteny from the Carditidae; however, the family may be polyphyletic, with some currently included taxa derived from other groups. There also remain some significant unresolved questions about which genera constitute the Condylocardiinae. For example, Chavan (1969: 549–550) placed *Carditella*, which has an external ligament as well as a central resilifer, in the Carditidae, but allocated *Carditopsis*, which has only a central resilifer, in the Condylocardiidae (op. cit., p. 558); they are otherwise very similar. Probably only molecular evidence will resolve this and similar questions, because miniaturization may have occurred more than once in the Carditidae, which, at least in substantial part, are brooders.

The Condylocardiidae is unexpectedly diverse, and in recent years many new species have been described, a significant number of them endemic to small geographic areas, particularly islands (Salas and Rolán, 1990; Salas and Cosel, 1991; Hayami and Kase, 1993; Middelfart, 2000, 2001, 2002a, b).

The purpose of the present study is to put on record the diversity of the Condylocardiidae in the tropical eastern Pacific, where there are several undescribed species, based on material that has recently become available.

All the species discussed here are under 3.1 mm in length, with most under 2 mm. Consequently, light photography is difficult, and the illustrations here were prepared with scanning electron microscopes at the California Academy of Sciences, the University of Southern California, and the Natural History Museum of Los Angeles County.

In the following treatment, each valid taxon is followed by a synonymy, description, information on type specimens and type localities, notes on distribution and habitat, the etymology of the new species names, and an additional discussion. The synonymies include all major accounts about the species, but not minor mentions in the literature. The distributional information is based on Recent specimens I have examined, except as noted. The only fossil occurrence was taken from the literature. References are provided in the Literature Cited for all works and taxa mentioned.

ABBREVIATIONS

The following abbreviations are used in the text: AM, Australian Museum, Sydney, Australia; CAS, California Academy of Sciences, San Francisco, California, USA; ICZN, International Commission on Zoological Nomenclature; INBio, Instituto Nacional de Biodiversidad, Santo Domingo, Herédia, Costa Rica; LACM, Natural History Museum of Los Angeles County, California, USA; PRI, Paleontological Research Institution, Ithaca, New York, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; UMML, Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, Miami, Florida, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMC, Zoologisk Museum Copenhagen, Denmark. Material in the private collections of Carol C. Skoglund,

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Table 1. Some key characters of eastern Pacific Condylocardiidae

	Shape	Radial/commarginal ribs	Prodissoconch	Hinge
Condylocardia digueti	narrow-trigonal	6–11 broad radials/commarginal bars	mucronate, with radial ribs, strongly demarcated	posterior lateral in LV low
Condylocardia hippopus	trapezoidal	7–8 radials, largest anteriorly/moderate commarginals	mucronate, with radial ribs, strongly demarcated	posterior lateral in LV large
Condylocardia sparsa	trapezoidal	4–5 broad radials, posterior slope unsculptured/commarginal striae	mucronate, with radial ribs, strongly demarcated	posterior lateral in LV large
Condylocardia fernandina	broad-trigonal	7–8 low radials/strong commarginals	mucronate, with radial ribs, strongly demarcated	posterior lateral in LV large
Condylocardia koolsae	ovate	15–16 radials/moderate commarginals	small, pointed, not set off	short posterior lateral in LV
Condylocardia elongata	elongate	9–10 radials, smallest medially/fine commarginals	pointed, not set off, tip indented	short posterior lateral in LV; each valve with large anterior cardinal
Condylocardia kaiserae	oblique-trapezoidal	13–14 radials, wider anteriorly/moderate commarginals	pointed, not set off, tip indented	posterior lateral in LV large
Condylocardia geigeri	ovate-trigonal	18 broad radials/crossbars ventrally	mucronate, set off, pustulose	posterior larger in LV; small in most specimens, large in largest specimens
Carditella galapagana	trapezoidal	16 nodose radials/fine commarginals	pointed, not strongly demarcated, pustulose	posterior lateral in LV large; each valve with large anterior cardinal
Carditella marieta	trapezoidal	11 nodose radials/fine commarginals	small, strongly demarcated, with fine radial sculpture	posterior lateral in LV large; each valve with large anterior cardinal

Phoenix, Arizona, USA; and Kirstie L. Kaiser, Puerto Vallarta, Jalisco, Mexico, was also examined.

MORPHOLOGICAL CHARACTERS

Aside from the fundamental difference in hinge morphology between the *Condylocardia* and *Carditella*, a combination of shell shape, external sculpture, prodissoconch morphology, and aspects of the dentition suffice to differentiate the species; these are detailed in the descriptions and the most important of them summarized in Table 1. Differences in shell color are also noted in the descriptions of some taxa.

Some of the taxa discussed here are provisionally placed in *Condylocardia* and may eventually merit the description of additional genera (Middelfart, personal communication, December 2002), a task beyond the scope of the present treatment (see also Discussion at end).

SYSTEMATICS

Condylocardiidae F. Bernard, 1896
Condylocardiinae F. Bernard, 1896

Condylocardia F. Bernard, 1896

Condylocardia F. Bernard, 1896: 195, ex Munier-Chalmas ms. Type species (subsequent designation by F. Bernard 1897: 175, as *C. pauliana* nom. van.): *C. sanctipauli* F. Bernard, 1896: 196, ex Munier-Chalmas ms. Recent, Île St. Paul, Indian Ocean.

Hippella Mörch, 1861: 200 (suppressed by ICZN, 1969: Opinion 872). Type species (monotypy): *Hippella hippopus* Mörch, 1861: 200. Recent, tropical eastern Pacific.

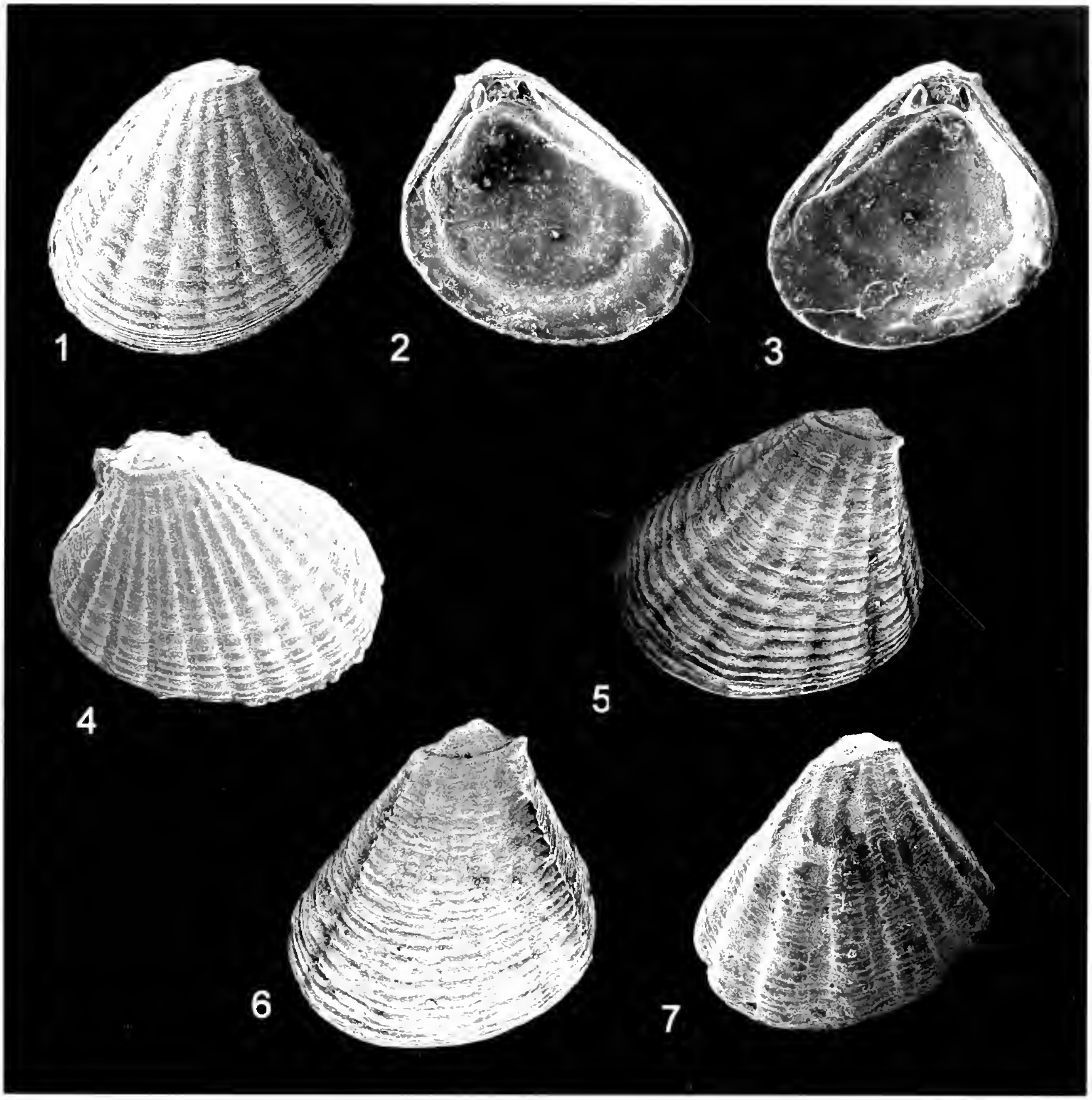
Radiocondyla Iredale, 1936: 272. Type species (original designation): *R. arizela* Iredale, 1936: 272, = *C. rectangularis* Cotton, 1930: 237–238, figure 10. Recent, Australia.

Diagnosis: Ligament in a central resilifer, no external ligament present. Prodissoconch bounded by a rim that is raised in most, and which has faint radial ribs in most. To 3.1 mm.

Condylocardia digueti Lamy, 1917
(Figures 1–7)

Condylocardia digueti Lamy, 1917: 443–445, figs. 1–3; 1922: 367–368, figs. 1–3; Hertlein and Strong, 1948: 106; Keen, 1958: 86–87, fig. 170; 1971: 110–111, fig. 245; Kaiser and Bryce, 2001: 15, pl. 7, fig. 1–1b.

Description: Shell narrow-trigonal, longer anteriorly; anterior end rounded to slightly pointed; posterior end rounded. Prodissoconch large, set off by raised rim, mucronate, with fine radial ribs. Lunule and escutcheon broad. Shell with 6–11 broad radial ribs with narrow interspaces, radial ribs crossed by commarginal bars. Pos-



Figures 1–7. *Condylocardia digueti.* **1–3.** External view of left valve, internal views of left and right valves, Bahia Magdalena, Pacific coast of Baja California Sur, Mexico, 1–11 m, LACM 71-183.13, lengths = 1.6 mm. **4.** External view of right valve, Bahia Pulmo, Baja California Sur, Mexico, 6 m, LACM 66-20.1, length = 1.5 mm. **5.** External view of left valve, Isla Santa Margarita, Pacific coast of Baja California Sur, 0–2 m, LACM 66-8.24, length = 1.5 mm. **6.** External view of left valve, Punta Ancon, Guayas, Ecuador, intertidal zone, LACM 70-12.40, length = 1.2 mm. **7.** Bahia San Gabriel, Isla Espiritu Santo, Baja California Sur, Mexico, syntype MNHN, left valve, length = 1.5 mm.

terior-most portion of posterior slope with commarginal bars only. White to light tan or yellow. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resilifer between them; elongate anterior lateral on submarginal ridge, separated from shell margin by serrate groove for anterior margin of left valve; posterior margin serrate, slightly raised distally into lateral tooth. Left valve with small, dorsally positioned anterior cardinal and large posterior cardinal, the resilifer between them; pit anterior to anterior cardinal for anterior cardinal of right valve; anterior margin with serrate lateral ridge, raised distally into low lateral tooth.

posterior margin with low lateral tooth on submarginal ridge separated by serrate groove for posterior margin of right valve. Length to 1.6 mm. Two specimens from Bahía Magdalena (LACM 71-183.43) (Figures 1–3), one specimen each from Bahía Pulmo (LACM 66-20.1) (Figure 4) and Isla Santa Margarita (LACM 66-8.24) (Fig. 5), both Baja California Sur, Mexico, and one specimen from Punta Ancón, Guayas, Ecuador (LACM 70-12.40) (Fig. 6), are figured here to show the range in shapes of this species.

Type Material: MNHN (no number), syntypes, 3 closed pairs, 2 right valves, 2 left valves, M. L. Diguet, 1914, from type locality. The largest left valve measures: length, 1.5 mm; height, 1.5 mm (Figure 7).

Type Locality: Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, Mexico (24.4° N, 110.4° W).

Distribution: NE end of Isla Cedros, Pacific coast of Baja California, 28.3° N [LACM 71-151.49, 71–152.31], into the Golfo de California as far N as Punta la Gringa, Bahía de Los Angeles, Baja California, 29.1° N [LACM 86-195.4], and Cabo Haro, Guaymas, Sonora, 27.8° N [CAS 159733], Mexico, to SE side of Punta Ancón, Peninsula de Santa Elena, Ecuador, 2.3° S (LACM 70-12.40; SBMNH 348087); Isla de Malpelo, Colombia (Kaiser Collection); Isla San Cristóbal, 0.9° N [LACM 34-267.2, 34-269.9, 38-188.3] and Isla Santa María, 1.3° N [LACM 34-297.3], Islas Galápagos, Ecuador; intertidal zone to 97 m (mean = 19.1 m; n = 87), in rubble. Lots examined: 91.

Discussion: The species is by far the most abundant and widespread in the eastern Pacific and exhibits considerable variability in shape and number of ribs. Most specimens, such as the figured syntype, are almost triangular, whereas others are more rounded, such as the specimen from Bahía Pulmo figured here. Available material fully bridges these extremes.

Condylocardia hippopus (Mörch, 1861)

(Figures 8–11)

Hippella hippopus Mörch, 1861: 200; Keen, 1958: 87; 1966: 6–8, fig. 4; 1971: 110–111, fig. 246 [*Condylocardia*].

Condylocardia panamensis Olsson, 1942: 186–187 [issue pagination = 34–35], 240 [= 88]; pl. 37 [= 3], figs. 9, 10; Hertlein and Strong, 1948: 106; Olsson, 1961: 190–191, 550, pl. 77, fig. 4; Keen, 1966: 8; 1971: 110 [as a synonym of *C. hippopus*]. PRI 4090, holotype, left valve; length 1.75 mm; PRI 4091, paratypes (neither lot examined). Zone of unconformity at base of Pleistocene, Punta de Piedra, Peninsula de Burica, Chiriqui Province, Panamá (8.2° N, 82.9° W).

Description: Shell trapezoidal, longer posteriorly, anterior end sharply rounded, posterior end narrow, pointed. Prodissoconch large, set off by raised rim, mucronate, with final radial ribs. Lunule narrow, shallow; escutcheon broad, concave. Shell with 7–8 radial ribs, larger and with wider interspaces posteriorly, and often with smaller radial rib posterior to these; posterior-most portion posterior slope without radial ribs. Radial ribs crossed by moderate commarginal ribs, forming bars on surfaces of radial ribs. White, sometimes with brown patches. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resilifer between them; anterior end with large lateral tooth on submarginal ridge separated by serrate groove for margin of right valve; posterodorsal margin serrate, swollen into low lateral tooth distally, with small submarginal shelf below it. Left valve with small, dorsally positioned anterior cardinal and large anterior cardinal, the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; anterodorsal margin serrate, slightly raised distally into lateral tooth, with small submarginal shelf below it; posterior end with lateral on small submarginal ridge separated from hinge margin by serrate groove for hinge margin of right valve. Length to 2.4 mm (LACM 72-42.60; Bahía Ballena, Puntarenas Province, Costa Rica). Two specimens from Bahía Potrero, Guanacaste Province, Costa Rica (LACM 72-38.28), are figured here (Figures 8–10).

Type Material: UZM no number, syntypes, one closed pair, one broken left valve, one intact left valve, one unusually thickened right valve, A. S. Oersted, 1848, from type locality, "in Margaritiferis" [text], "in Balan" [label]. The intact left valve is figured here, length 2.0 mm; height 1.9 mm (Figure 11). An external view of the right valve of the pair was given by Keen (1966: 7, figure 4).

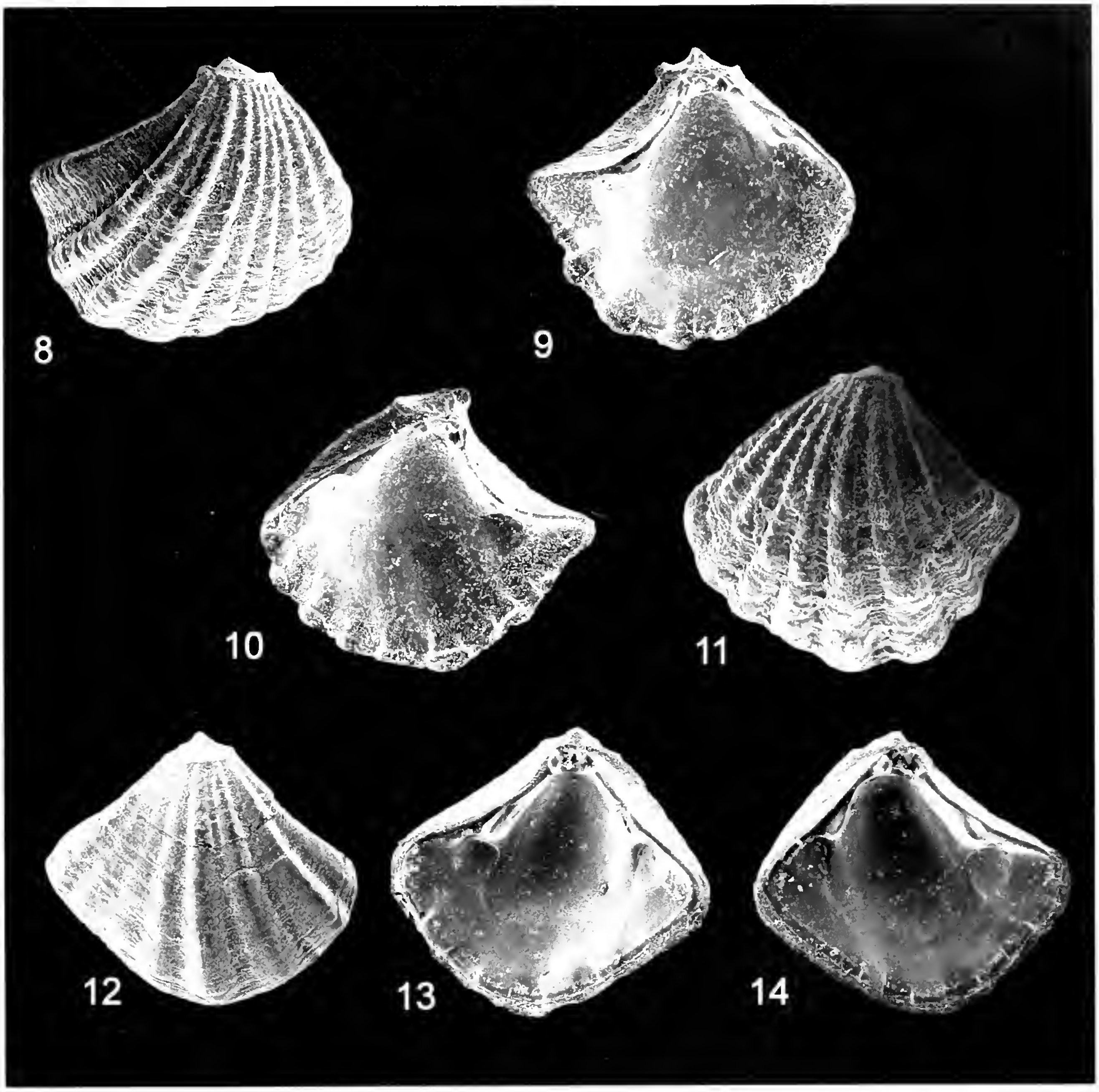
Type Locality: Puntarenas, Puntarenas Province, Costa Rica, 10.0° N, 84.9° W.

Distribution: Bahía Jobo, Guanacaste Province, 11.1° N [LACM 72-17.43], to Isla del Caño, Puntarenas Province, 8.3° N [LACM 72-63.78], Costa Rica; Búcaro, Los Santos Province, Panamá, 7.4° N (Olsson, 1961; specimens not located in UMML (N. Voss, personal communication, 18 September 2001); Isla Taboga, Panamá Province, 8.8° N [LACM 39-262.1], Panamá; Isla Marchena, Islas Galápagos, Ecuador, 0.3° N [LACM 34-285.7]; 3-99 m (mean = 23.7 m; n = 24), in rubble. Lots examined: 25

Condylocardia sparsa new species

(Figures 12–14)

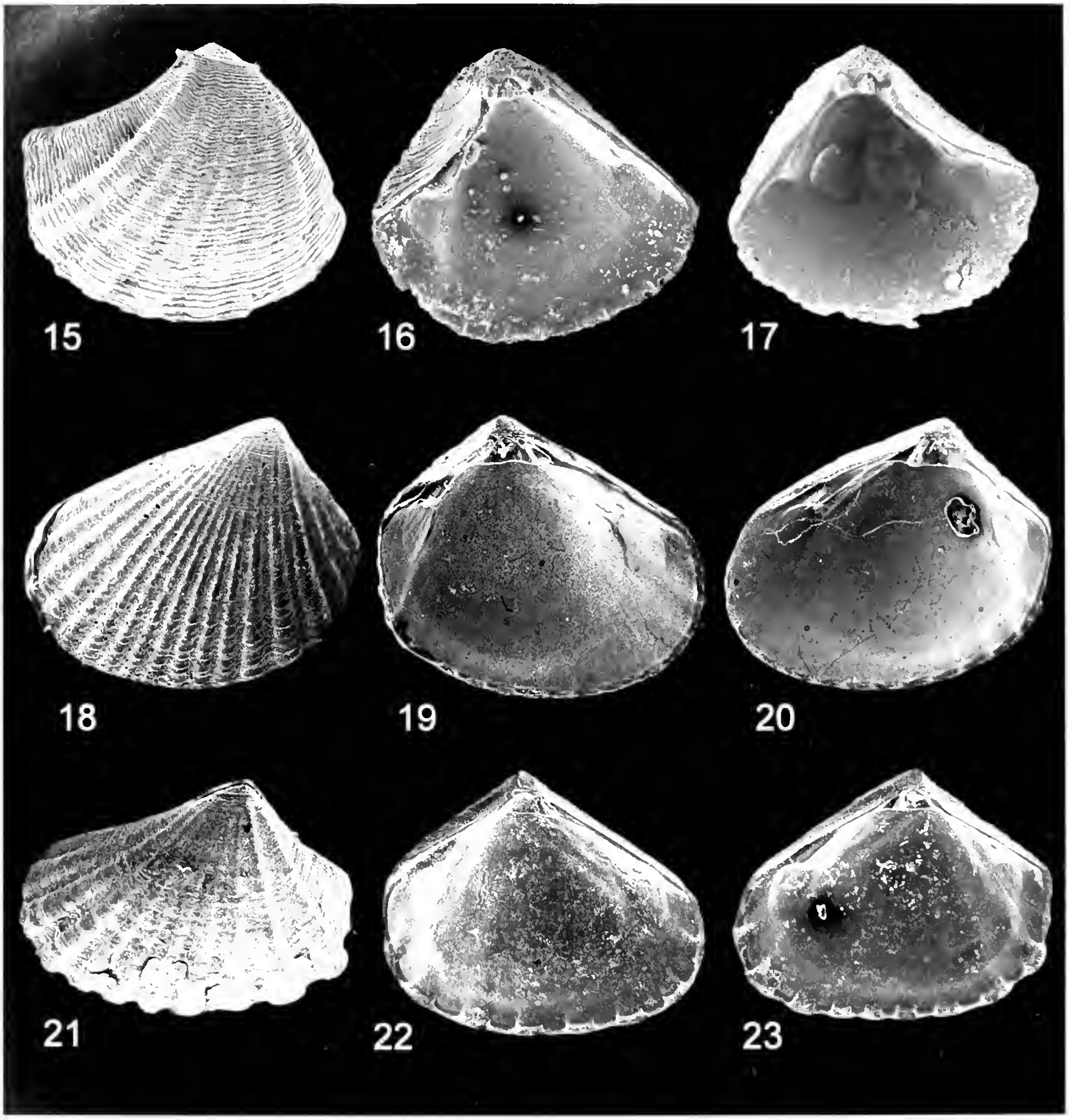
Description: Shell trapezoidal, longer posteriorly, inflated; anterior end produced, pointed, posterior end pointed. Prodissoconch large, set off by raised rim, mucronate, with fine radial ribs. Lunule broad, concave; escutcheon broad, less concave. Shell with 4–5 broad radial ribs on the anterior and central slopes, interspaces of approximately half rib width; posterior slope with only faint traces of radial ribs; ribs crossed by commarginal growth striae. Beaks and anterior slope brown, but shell entirely brown in some specimens. Right valve with moderate anterior cardinal and tiny, dorsally positioned posterior cardinal, the resilifer between them; posterior



Figures 8–14. *Condylocardia* species. **8–11.** *Condylocardia hippopus*. **8–10.** External view of right valve; internal views of left and right valves, Bahia Potrero, Guanacaste Province, Costa Rica, 8–12 m, LACM 72-38.28; lengths = 1.8 mm. **11.** Puntarenas, Puntarenas Province, Costa Rica, syntype, UZM, left valve; length = 2.0 mm. **12–14.** *Condylocardia sparsa* new species, paratypes, external view of right valve; internal views of left and right valves, Bahia Potrero, Guanacaste Province, Costa Rica, 8–12 m, LACM 2919, locality 72-38; lengths = 1.9 mm (external view), 1.7 mm (internal views).

to posterior cardinal is pit for posterior cardinal of left valve; anterior end with elongate lateral on submarginal ridge separated from hinge margin by serrate groove for margin of left valve; posterodorsal margin raised into lateral tooth distally, with very short submarginal shelf directly below it. Left valve with tiny, dorsally positioned anterior cardinal and moderate posterior cardinal, the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; anterior end with lateral tooth on hinge margin and very short submarginal shelf directly below it; posterior end with large lateral on submarginal ridge separated from hinge margin by serrate groove for margin of right valve. Length to 2.2 mm (LACM 80-60.16).

Type Material: LACM 2918, holotype, pair, length



Figures 15–23. *Condylocardia* species. **15–17.** *Condylocardia fernandina*, new species, paratypes; external view of right valve, internal [illegible] of left and right valves; Isla Marchena, Islas Galápagos, Ecuador, 12 m; LACM 2921; locality 66-125; lengths = 1.9 mm (external), 1.7 mm (internal views). **18–20.** *Condylocardia koolsae*, new species, paratypes; external view of left valve, internal views of left [illegible] valves; Isla Wolf, Islas Galápagos, Ecuador, 274 m; LACM 2925; locality 31-264; lengths = 2.0 mm. **21–23.** *Condylocardia* [illegible], new species, paratypes; external view of left valve, internal views of left and right valves; Isla Fernandina, Islas Galápagos, Ecuador, 5–40 m; LACM 2927; locality LACM 72-196; lengths = 1.9 mm (external view), 2.0 (internal views).

1.9 [illegible] 1.7 mm; LACM 2919, paratypes, 10 [illegible] station 126, Pat LaFollette and Don Cadien, 10 February 1972, from type locality. Two paratypes [illegible] here (Figures 12–14).

Type Locality: Punta Pencas, N of Bahía Potrero, Guanacaste Province, Costa Rica, 10°29'15" N, 85°48'55" W; LACM locality 72-38, 8–12 m, Searcher station 126.

Distribution: Isla Meanguera, El Salvador, 13.2° N, to Punta Quepos, Costa Rica, 9.4° N; intertidal zone to 35 m (mean = 12.1 m; n = 11).

Other Material Examined: El Salvador: Kaiser Collection and LACM 2001-15.1, Isla Meanguera, La Unión Province, El Salvador, 13.2° N, 1 m, 3 pairs, 8 valves; Kaiser Collection, Isla Meanguera, La Unión Province, El Salvador, 13.2° N, 5 m, 17 pairs, 8 valves; Kaiser Collection and SBMNH 346013, Isla Meanguera, La Unión Province, El Salvador (13.2° N), 12 m, 53 pairs, 32 valves; Nicaragua: LACM 74-86.12, El Velero, Leon Province, Nicaragua, 12.0° N, 2 m, 3 beachworn valves; Costa Rica: LACM 80-60.16, Cabo Santa Elena, Puntarenas Province, Costa Rica, 10.8° N, intertidal zone, 1 pair; Type lot, near Bahía Potrero, Guanacaste Province, Costa Rica, 10.5° N, LACM locality 72-38, 8–12 m; INBio 0003404072, Cabo Blanco, Puntarenas Province, Costa Rica, 9.6° N, 20–50 m, 1 pair, 4 valves; INBio 0001494861, Punta El Flor, near Cabo Blanco, Puntarenas Province, Costa Rica, 9.6° N, 14 m, 1 pair, 2 valves; SBMNH 348088, Bahía Ballena, Puntarenas Province, Costa Rica, 9.7° N, 12–14 m; LACM 72-58.58, Punta Quepos, Puntarenas Province, Costa Rica, 9.4° N, 9–23 m, 12 pairs, 1 valve (plus one pair now in AM C.403166); LACM 72-59.29, Punta Quepos, Puntarenas Province, Costa Rica, 9.4° N, 23 m, 1 pair.

Etymology: The specific name refers to the few radial ribs on this species.

Discussion: This species is most similar to the sympatric *C. hippopus*, differing in being more trapezoidal, more inflated, and with relatively unsculptured posterior slope. *Condylocardia sparsa* also has fewer radial ribs, which are crossed by commarginal striae rather than ribs.

Condylocardia fernandina new species
(Figures 15–17)

Description: Shell broad-trigonal, subequilateral; anterior end pointed; posterior end sharply rounded. Prodissoconch large, set off by raised rim, mucronate, with fine radial ribs. Lunule broad, concave; escutcheon broad, flat. Shell with 7–8 low, broad radial ribs, often with small radial rib anterior to these; interspaces narrow, the anterior-most wider; ribs crossed by dense, moderately strong commarginal ribs; shell white to brown. Right valve with moderate anterior cardinal and very small, dorsally positioned posterior cardinal, the resilifer between them; posterior to posterior cardinal is pit for posterior cardinal of left valve; anterior end with lateral on submarginal ridge separated from shell margin by serrate groove for margin of left valve; posterior margin serrate, elevated distally into lateral tooth, with short submarginal shelf directly below it. Left valve with tiny, dorsally positioned anterior cardinal and moderate posterior cardinal, the resilifer between them; anterior to anterior cardinal is pit for anterior cardinal of right valve; anterior margin serrate, raised distally into lateral tooth, with short submarginal shelf directly below it; posterior margin with strong lateral on submarginal ridge, separated from shell margin by serrate groove for posterior margin of right valve. Length to 2.1 mm.

Type Material: LACM 2920, holotype, pair, length 1.9 mm, height, 1.8 mm; LACM 2921, paratypes, 7 pairs, 14 valves; AM C.403167, paratype, left valve, James H. McLean, 11 May 1984, from type locality. Two paratypes are figured here (Figures 15–17).

Type Locality: Punta Espejo, E side of Isla Marchena, Islas Galápagos, Ecuador 0°19.5′ N; 90°24′ W, LACM locality 84-26, 12 m, rock and coarse sand.

Distribution: Islas Galápagos, Ecuador, from 1.4° N to 1.4° S; not counting the uncertain lot from Isla Wolf, 0–110 m (mean = 33.1 m; n = 8).

Other Material Examined: Restricted to the Islas Galápagos, Ecuador: LACM 34-264.6, Isla Wolf, 1.4° N 274 m, 1 pair [specimen tentatively assigned to this species]; LACM 84-39.33, S anchorage, Isla Pinta, 0.6° N, intertidal zone, rocks and sand, 1 pair; LACM 84-41.19, S side of Isla Pinta, 0.5° N; 15–24 m, rocky slope, 3 valves; LACM 84-26.16, type lot, Isla Marchena, 0.3° N, 12 m; LACM 66-125.34, N of Punta Espinosa, Isla Fernandina, 0.3° S, 0–3 m, 1 pair; CAS 42344, Bahía Conway, Isla Santa Cruz, 0.5° S, depth not recorded, 12 pairs, 17 valves; LACM 34-287.7, Bahía Academy, Isla Santa Cruz, 0.8° S, 27 m, 7 valves; LACM 34-267.3, Bahía Wreck, Isla San Cristóbal, 0.9° S, 40 m, 1 pair; LACM 33-161.2, Hancock Bank, NE of Isla Santa María, 1.0° S, 110 m, 1 valve; LACM 34-283.10, Isla Española, 1.4° S, 55 m, 1 pair, 7 valves.

Etymology: The specific name is taken from Isla Fernandina, Islas Galápagos, where the species was first noted.

Discussion: The lot from Isla Wolf consists of a single, worn pair that is thinner, broader, and flatter than the rest of the referred material. Of eastern Pacific species, *Condylocardia fernandina* is most similar to *C. digueti*, differing from it in attaining a larger size, in being nearly equilateral, broader, with more pointed ends. The sculpture is similar but heavier, the radial ribs being more raised. The commarginal sculpture is much finer and denser. The prodissoconch is more mucronate. Of western Atlantic species, it is most similar to *C. smithi* (Dall, 1896: 16–17, pl. 1, figure 4, as *Carditella*), described from Bermuda, in having a trigonal shape and dense, lamellar sculpture, but it differs in being larger and in having fewer, more prominent ribs (based on examination of USNM 762566 from Bermuda).

Condylocardia koolsae new species
(Figures 18–20)

Description: Shell ovate, longer anteriorly; anterior end rounded; posterior end subtruncate, sharply rounded posterodorsally. Lunule elongate; escutcheon broad. Prodissoconch small, pointed, set off by an inconspicuous rim. Sculpture of 15–16 radial ribs, broadest just anterior to posterior slope; interspaces widest towards ends; with moderate commarginal ribs, forming knobs on radial ribs; posterior-most portion of posterior slope with commarginal striae only. White. Right valve with elongate anterior cardinal and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior lateral on submarginal ridge separated by groove for lateral of left valve; posterior margin slightly elevated into lateral tooth distally, with short submarginal shelf below it. Left valve with elongate anterior cardinal, fitting above that of right valve, and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior shell margin slightly elevated distally into lateral tooth, short submarginal shelf below it; short posterior lateral present on submarginal ridge separated from shell margin by groove for margin of right valve. Length to 2.2 mm.

Type Material: LACM 2924, holotype, pair; length, 2.2 mm; height, 1.9 mm. LACM 2925, paratypes, 5 pairs, 11 valves; AM C.403169, paratype, right valve. VELERO III, Alan Hancock Foundation station BS 430, 14 January 1934, all from type locality. Two of the LACM paratypes are figured here (Figures 18–20).

Type Locality: Isla Wolf, Islas Galápagos, Ecuador, 1°23′ N, 91°49′ W; Alan Hancock Foundation station BS 430, LACM locality 34-264, 274 m, mud. This is the same station as the type locality of *Carditella galapagana*.

Distribution: Known only from Isla Wolf, Islas Galápagos, Ecuador, 1.4° N; 183–274 m (mean = 228.5 m; n = 2).

Other Material Examined: Type lot, Isla Wolf, Islas Galápagos, Ecuador, 1.4° N, LACM locality 34-264, 274 m; LACM 34-263.7, same locality, 183 m, 3 pairs, 3 valves.

Etymology: This species is named after Elizabeth Kools of the California Academy of Sciences, who has helped on this and many other projects.

Discussion: In this species and *C. elongata*, unlike in other eastern Pacific species of *Condylocardia*, the larger tooth in the left valve is the anterior one, which fits above the anterior cardinal of the right valve.

Condylocardia elongata new species
(Figures 21–23)

Description: Shell elongate, longer anteriorly; anterior end rounded, posterior end truncate. Prodissoconch small, pointed, unsculptured, set off by an inconspicuous rim; tip indented. Lunule elongate, of moderate width; escutcheon broad, slightly concave. Sculpture of 9–10 strong radial ribs on anterior and central slopes, ribs with narrower interspaces medially; radial ribs crossed by fine commarginal striae, but with nodes on posterior-most radial rib. Posterior-most portion of posterior end with commarginal striae only. White to light tan. Right valve with narrow anterior cardinal and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior end with triangular lateral on submarginal ridge separated from shell margin by serrate groove for anterior margin of left valve; posterodorsal margin elevated into low lateral tooth. Left valve with narrow anterior cardinal, fitting above that of the right valve, and minute, dorsally positioned posterior cardinal, the resilifer between them; anterior end serrate, with low lateral tooth on hinge margin, and tiny submarginal ridge; posterodorsal margin with lateral tooth on submarginal ridge separated from hinge margin by groove for posterior lateral of right valve. Length to 2.4 mm (a paratype).

Type Material: LACM 2926, holotype, pair; length, 2.0 mm; height, 1.6 mm. LACM 2927, paratypes, 5 pairs, 21 valves, SEARCHER station 331, 25 January 1972. Two paratypes are figured here (Figures 21–23).

Type Locality: Punta Espinosa, Isla Fernandina, Islas Galápagos, Ecuador, 0°16′5″ S, 91°26′20″ W; LACM locality 72-196, SEARCHER station 331, 15–30 m.

Distribution: Islas Galápagos, Ecuador, from 1.4° N to 1.3° S, with a possible specimen from Isla La Plata, Ecuador.

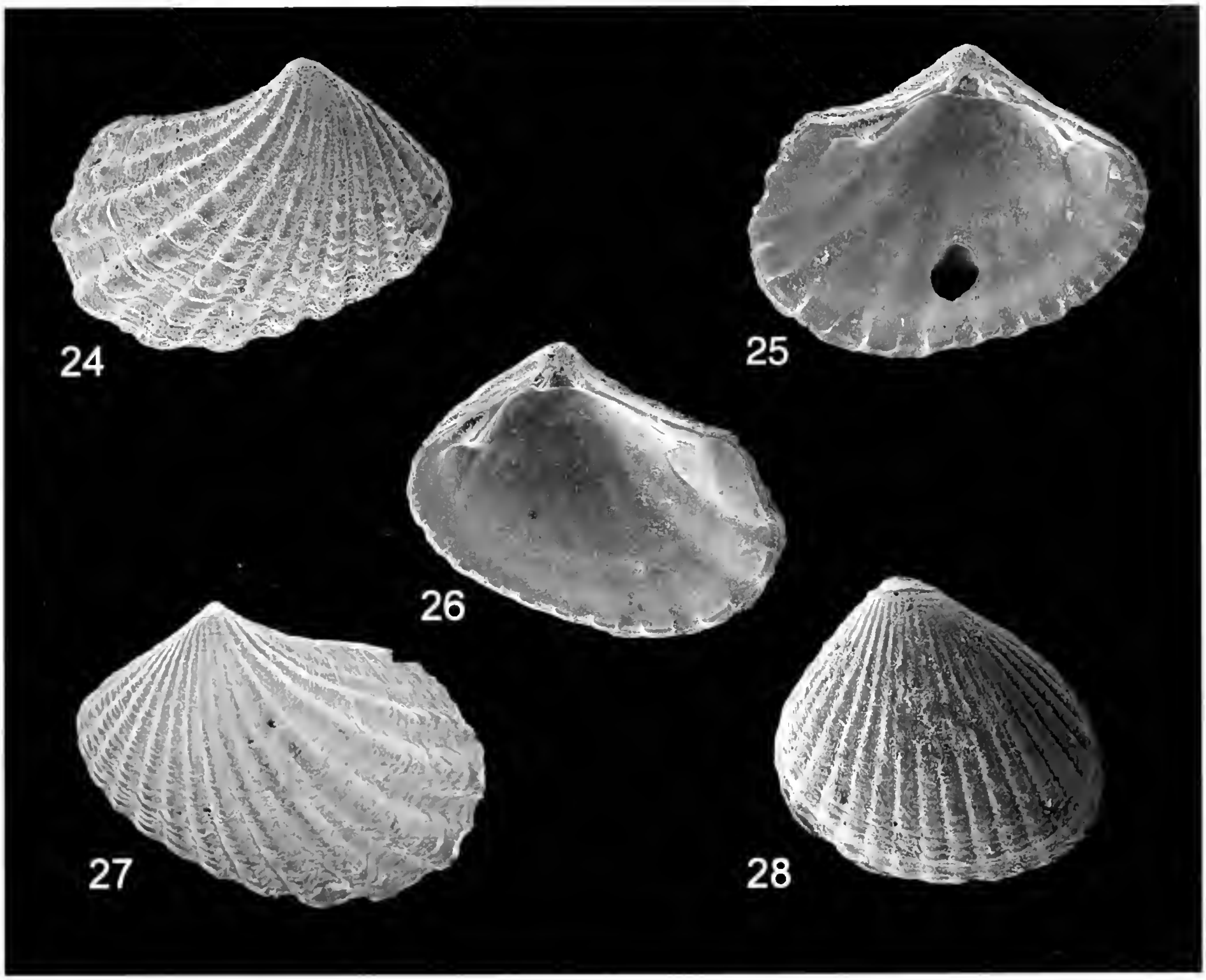
Other Material Examined: All from the Islas Galápagos, Ecuador, except the last: LACM 34-264.8, Isla Wolf, 1.4° N, 274 m, 1 valve; LACM 34-263.8, same locality, 183 m, 2 valves; LACM 84-41.20, S side of Isla Pinta, 0.5° N, 15–24 m, 1 pair, 11 valves; LACM 84-26.17, Punta Espejo, E side of Isla Marchena, 0.3° N, 12 m, 6 pairs, 10 valves; LACM 33-174.9, Bahía Darwin, Isla Genovesa, 0.3° N, 31 m, 4 pairs, 37 valves; LACM 34-262.2, Punta Albemarle, Isla Isabela, 0.2° S, 31 m, 1 pair; Type lot, Punta Espinosa, Isla Fernandina, 0.3° S, LACM locality 72-196, 15–30 m; LACM 34-271.9, Bahía Sullivan, Isla San Salvador, 0.3° S, 37 m, 3 valves; LACM 34-287.8, Bahía Academy, Isla Santa Cruz, 0.8° S, 27 m, 7 valves; LACM 38-193.15, same locality, 0.8° S, 18–37 m, 4 valves; LACM 33-157.7, Bahía Post Office, Isla Santa María, 1.3° S, 46 m, 1 valve; LACM 34-283.11, Isla Española, 1.4° S, 55 m, 2 pairs, 10 valves; SBMNH 348089, Isla la Plata, Manabí Province, Ecuador, 1.3° S, 12–30 m, 1 valve [specimen tentatively assigned to this species] Thus, 12–274 m (mean = 58.2 m; n = 13). Lots examined: 13.

Etymology: The specific name refers to the fact that this species is unusually elongate for the genus.

Discussion: *Condylocardia elongata* and *C. koolsae* are unique among eastern Pacific species of *Condylocardia* in that the larger cardinal tooth in the left valve is the anterior one.

Condylocardia kaiserae new species
(Figures 24–27)

Condylocardia sp. 1.—Kaiser and Bryce, 2001: 45, pl. 7, figures 2, 2a, 2b.



Figures 24–28. *Condylocardia* species. **24–27.** *Condylocardia kaiserae* new species, paratypes. **24–26.** External view of right valve, internal views of left and right valves, Isla Marchena, Islas Galápagos, Ecuador, 12 m, LACM 2929 (locality 84-26), lengths = 2.4 mm (external view), 2.1 mm (internal views). **27.** External view of left valve, "Tiger Mount", Isla de Malpelo, Colombia, 41–44 m, SBMNH 346012, length = 2.2 mm. **28.** *Condylocardia geigeri* new species, paratype, external view of right valve, Isla Santa Cruz, Islas Galápagos, Ecuador, 18 m, LACM 2964 (locality 34-286), length = 1.3 mm.

Description: Shell oblique-trapezoidal, much longer posteriorly; anterior end sharply rounded, posterior end broadly rounded. Prodissoconch large, pointed, mucronate, demarcated by rim, with fine radial ribs; tip indented. Lunule narrow; escutcheon broad, slightly concave. Sculpture of 11–14 radial ribs, widest posterior to midline with wider interspaces, becoming narrower anteriorly, but also with 1–2 narrow posterior ribs; posterior-most part of posterior slope with commarginal ribs only. Radial ribs crossed by moderate commarginal ribs, forming nodes on radial ribs, slightly scabrose in some specimens. White to light tan, posterior slope with brown patches in some specimens. Right valve with and large anterior cardinal and minute, dorsally placed posterior cardinal, the resilifer between them; anterodorsal margin with lateral tooth on submarginal ridge, separated from shell margin by groove for shell margin of left valve; posterior margin raised into slightly serrate lateral tooth distally. Left valve with minute, dorsally positioned anterior cardinal and large posterior cardinal, the resilifer between them; anterior margin raised distally into low, serrate lateral tooth, with narrow submarginal shelf for margin of right valve directly below it; posterior end with large lateral on submarginal ridge, separated from hinge margin by groove for margin of right valve. Length to 3.1 mm (Isla Darwin, Islas Galápagos, LACM 84-29.23).

Type Material: LACM 2928, holotype, pair; length, 2.2 mm; height, 1.7 mm. LACM 2929, paratypes, 21 pairs, 7 valves; AM C.403173, paratypes, 1 right valve, 1 left valve. James H. McLean, 11 May 1984. Two paratypes are figured here (Figures 24–26). SBMNH 346012, paratype; length, 2.2 mm (Figure 27) ["Tiger Mount", Isla de Malpelo, Colombia, 4.0° N, 81.6° W, 41–44 m; Kirstie L. Kaiser; 11 March 2000].

Type Locality: Punta Espejo, E side of Isla Marchena, Islas Galápagos, Ecuador, 0°19.5′ N, 20°21′ W, LACM locality 84-26, 12 m, rock and coarse sand.

Distribution: Isla de Malpelo, Colombia, 4.0° N, and Islas Galápagos, Ecuador, as far south as 1.4° S; 12–274 m (mean = 77.4 m; n = 16).

Other Material Examined: Material from Isla de Malpelo, Colombia: Kaiser Collection, "Tiger Mount", 4.0° N, 9–18 m, 52 pairs, 15 valves; Kaiser Collection and LACM 2000-180.1, "Tiger Mount", 4.0° N, 24–34 m, 56 pairs, 10 valves; Kaiser Collection, "Tiger Mount", 4.0° N, 30–56 m, 12 pairs, 16 valves; Kaiser Collection and SBMNH 346012, "Tiger Mount", 4.0° N, 11–44 m, 2 pairs, including the paratype cited above. Material from the Islas Galápagos, Ecuador: LACM 84.29.23, N side of Arch Rock, SE end of Isla Darwin, 1.6° N, 6–9 m, boulders, coral and *Caulerpa*, 2 pairs, 6 valves; LACM 34-263.5, Isla Wolf, 1.4° N, 183 m, 1 pair, 9 valves; LACM 34-264.9, Isla Wolf, 1.4° N, 274 m, 1 pair, 5 valves; LACM 84-33.18, W anchorage, Isla Wolf, 1.4° N, 9–23 m, rocky slope, 1 valve; LACM 84-28.22, Beyond SW anchorage, Isla Wolf, 1.4° N, 23–30 m, sand, 1 pair, 6 valves, LACM 84-26.18; Type locality, Isla Marchena, 0.3° N, LACM locality 84-26, 12 m; LACM 34-43.23, Bahía Stephens, Isla San Cristóbal, 0.8° S, 59 m, 2 valves; LACM 33-161.3, Hancock Bank, Isla Santa María, 1.1° S, 110 m, 1 valve; LACM 34-280.5, Bahía Post Office, Isla Santa María, 1.3° S, 16 m, 1 valve; LACM 34-281.8, same locality, 1.2° S, 119 m, 7 valves; LACM 34-282.11, Bahía Gardner, Isla Española, 1.4° S, 64 m, 9 valves; LACM 34-283.9, Isla Española, 1.4° S, 55 m, 2 pairs, 3 valves.

Etymology: This species is named for Kirstie L. Kaiser, who has specialized on tropical eastern Pacific island faunas and encountered the first specimens of this species at Isla de Malpelo, Colombia.

Discussion: It is possible to confuse this species with very small specimens of the lucinid genus *Ctena*. The latter are longer anteriorly, have somewhat sunken ligament posteriorly and no central resilifer, two strong cardinal teeth in each valve, subequal anterior and posterior lateral teeth in the left valve, and a bulbous prodissoconch.

Condylocardia geigeri new species
(Figure 28)

Description: Shell ovate-trigonal, longer anteriorly; anterior end rounded, posterior end subtruncate. Prodissoconch small, set off by raised rim, mucronate, pustulose, without radial ribs. Lunule broad, escutcheon broad. Shell with approximately 18 broad radial ribs with narrow interspaces. Radial ribs with cross-bars, most conspicuously ventrally. White to light brown. Right valve with large anterior cardinal and small, dorsally positioned posterior cardinal, the resilifer between them; without pit for posterior cardinal of left valve; anterior end with lateral on short submarginal ridge separated from hinge margin by groove for hinge margin of left valve; posterodorsal margin slightly pustulose, raised distally into small lateral tooth. Left valve with small, dorsally positioned anterior cardinal and large posterior cardinal, the resilifer between them; anterodorsal margin slightly pustulose, raised distally into low lateral tooth; posterior end with small lateral tooth on submarginal ridge, becoming more conspicuous in the largest specimens. Length to 1.9 mm (a paratype).

Type Material: LACM 2962, holotype, pair; length, 1.3 mm; height, 1.2 mm; LACM 2963, paratypes, 55 pairs, 97 valves, VELERO III, Allan Hancock Foundation station BS 439, 24 January 1934, LACM 2964, paratype, right valve, length, 1.3 mm [LACM locality 34-286; Bahía Academy, Isla Santa Cruz, Islas Galápagos, Ecuador, 0.8° S, 18 m (Fig. 28); 1 closed pair and 5 additional valves specimens from this lot are contained in LACM 34-286.2].

Type Locality: Bahía Sullivan, Isla San Salvador, Islas Galápagos, Ecuador, 0°16′ S, 90°34′ W, Allan Hancock Foundation station BS 439, LACM locality 34-271, 37 m.

Distribution: Islas Galápagos, Ecuador from 0.2° S to 1.3° S, 16–124 m (mean = 51.4 m; n = 18).

Other Material Examined: Islas Galápagos, Ecuador: LACM 33-164.4, Bahía James, Isla San Salvador, 0.2° S, 27 m, 9 valves; LACM 34-273.8, same locality, 44 m, 2 valves; LACM 34-277.6, same locality, no depth recorded, 1 valve; LACM 34-289.8, same locality, 29 m, 3 pairs, 30 valves; Type locality, Bahía Sullivan, Isla San Salvador, 0.3° S, LACM locality 34-271, 37 m; LACM 33-174.10, Bahía Darwin, Isla Genovesa, 31 m, 2 valves, LACM 33-175.1, Isla Seymour, 0.4° S, 24 m, 2 pairs, 5 valves, LACM 34-268.1, Isla Seymour, 0.5° S, no depth recorded, 1 pair, 3 valves; LACM 34-292.3, Isla Seymour, 0.5° S, no depth recorded, 2 pairs, 8 valves; LACM 33-169.3, N of Isla Santa Cruz, 0.5° S, 124 m, 1 pair; LACM 33-170.6, same locality, 101 m, 1 valves; LACM 33-171.4, same locality, 64 m, 1 valve; LACM 33-172.3, same locality, 124 m, 3 valves, LACM 33-173.3, same locality, 101 m, 1 pair, 11 valves; LACM 33-166.8, N of Isla Pinzón, 0.6° S, 82 m, 2 valves, LACM 38-191.3, Bahía Cartago, Isla Isabella, 0.6° S, 22 m, 2 valves, LACM 34-286.2, Bahía Academy, Isla Santa Cruz, 0.8° S, 16 m, 1 pair, 5 valves, plus figured paratype; LACM 34-287.9, same locality, 27 m, 11 pairs, 26 valves, many juveniles, LACM 38-193.16, same locality, 18–37 m, 5 valves, LACM 34-270.6, Isla San Cristóbal, 0.8° S, no depth recorded, 7 valves, LACM 33-157.8, Bahía Post Office, Isla Santa María, 1.3° S, 16 m, 2 valves.

Etymology: This species is named for Daniel L. Geiger, a research associate of the Santa Barbara Museum of Natural History, who has been helpful on many projects.

Discussion: This species is closest to *Condylocardia digueti*, differing in having many more radial ribs and in being more ovate.

POSSIBLE ADDITIONAL SPECIES OF *CONDYLOCARDIA*

One lot contain specimens that do not fit the species described above, but there is too little material is available to propose an additional new taxon at this time: LACM 84-29.24, N side of Arch Rock, SE end of Isla Darwin, Islas Galápagos, Ecuador (1.6° N); 6–9 m. Lot contains 1 open pair and 2 valves, all somewhat worn. The shells are slightly longer and somewhat truncate anteriorly, with 12–13 elevated, nodose ribs.

Carditella E. A. Smith, 1881: 42–43

Type species: (subsequent designation by Dall, 1903: 702): *C. pallida* E. A. Smith, 1881: 43, pl. 5, figure 9–9b. Recent, Estrecho de Magellanes, Chile. Medium sized to minute (up to 5.2 mm). With central resilifer as well as a sunken external ligament that is substantial in some species and minute in others. The following two species are placed in *Carditella* because of their small external ligaments in addition to a resilifer.

Carditella galapagana new species
(Figures 29–32)

Condylocardia sp. 2—Kaiser and Bryce, 2001: 45, pl. 7, figures 3, 3a, 3b.

Description: Shell trapezoidal, longer posteriorly; anterior end sharply rounded; posterior end subtruncate. Prodissoconch small, pointed, not strongly demarcated, pustulose, its tip rounded to flattened. Lunule narrow; escutcheon elongate, wider in right valve. Sculpture of 16–17 strong radial ribs; interspaces half as wide as ribs; radial ribs nodose, crossed by moderate commarginal ribs, forming nodes on rib surfaces. White. Right valve with broad anterior cardinal; resilifer separated from sunken external ligament by low ridge that is slightly swollen dorsally into minute tooth; anterior end with triangular lateral tooth on submarginal ridge, separated from shell margin by groove for margin of left valve; anterior valve margin between beaks and distal lateral tooth granular. Left valve with large anterior cardinal, which fits above anterior cardinal of right valve, and narrow ridge on anterior border of resilifer; resilifer separated from sunken external ligament by low ridge, swollen dorsally into minute tooth, anterior lateral on hinge margin, the area between it and beaks granular; posterodorsal margin with lateral on submarginal ridge separated by serrate groove for margin of right valve. Length to 2.6 mm (a paratype valve).

Type Material: LACM 2930, holotype, pair; length, 1.9 mm; height, 1.7 mm. LACM 2931, paratypes, 3 pairs, approximately 108 valves; AM C.403175, paratypes, 1 right valve, 1 left valve; all VELERO III, Alan Hancock Foundation station BS 430, 11 January 1934, from type locality. Two paratypes are figured here (Figures 28–31).

Type Locality: Isla Wolf, Islas Galápagos, Ecuador, 1°23′ N, 91°49′ W, Alan Hancock Foundation station BS 430; LACM locality 34-264, 183–274 m, mud. This is the same station as the type locality of *Condylocardia koolsae*.

Distribution: Isla de Malpelo, Colombia, 4.0° N, to Islas Galápagos, Ecuador, as far south as 0.5° S; approximately 29–228 m (mean = 151 m; n = 4).

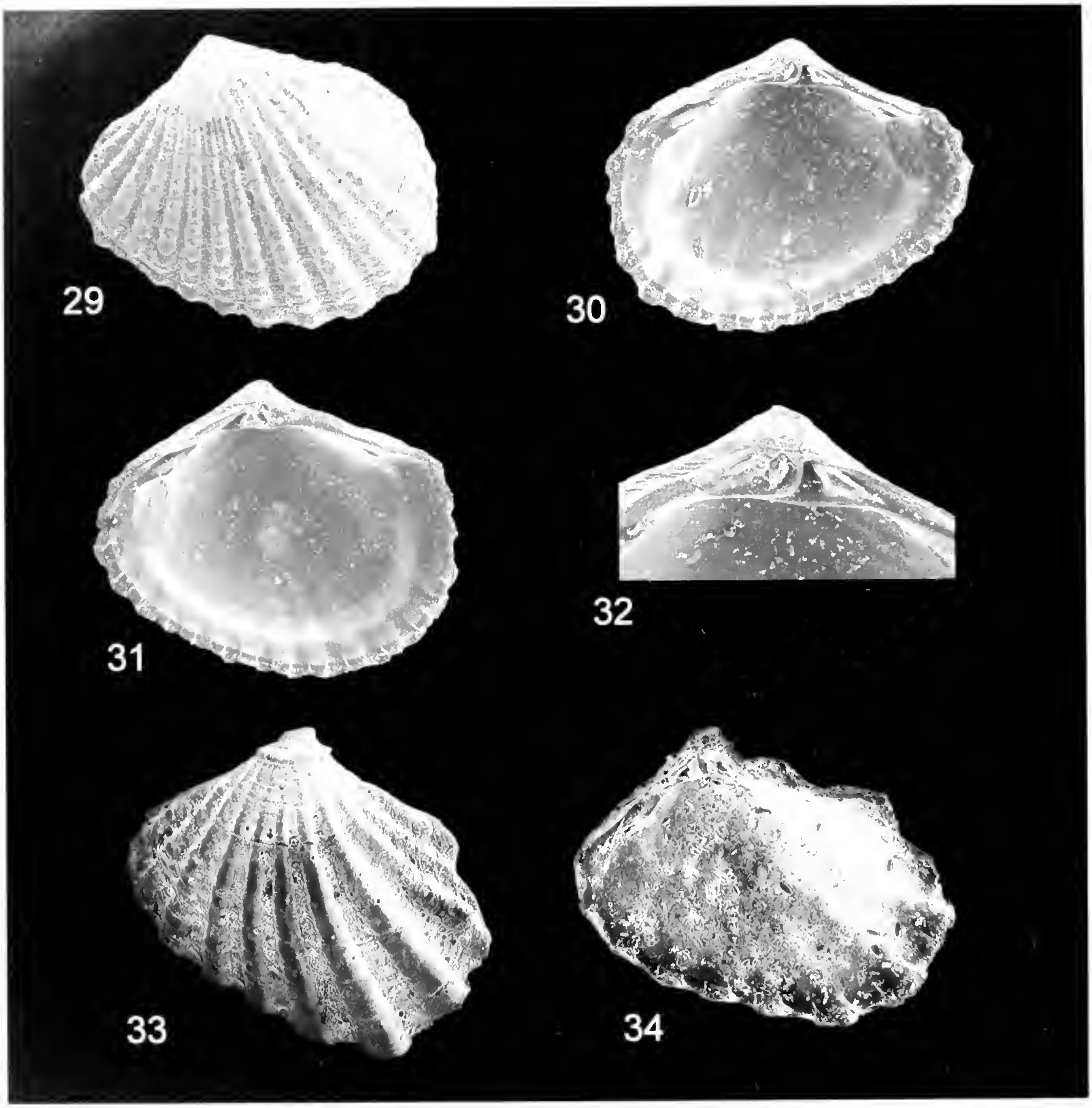
Other Material Examined: Kaiser Collection, "Tiger Mount", Isla de Malpelo, Colombia, 4.0° N; 24–34 m, 4 valves. Material from the Islas Galápagos, Ecuador: LACM 34-263.6, Isla Wolf, 1.4° N, 183 m, 2 valves; Type locality, Isla Wolf, 1.4° N, LACM locality 34-264, 183–274 m; LACM 34-265.13, Tagus Cove, Isla Isabela, 0.3° S, 146–183 m, 8 pairs, 90 valves; LACM 34-270.5, Isla San Cristóbal, 0.5° S, no depth recorded, three tiny valves [specimens tentatively assigned to this species].

Etymology: The specific name refers to the Islas Galápagos, Ecuador.

Discussion: This species is somewhat similar to but has more radial ribs than *C. hawaiensis* Dall, Bartsch and Rehder, 1938 (p. 120, pl. 33, figures 5–8), which has only about 11 (Kay, 1979: 553, figure 180E, 554). It differs from the Peruvian-Chilean *Carditella tegulata* (see list below) in being more quadrate and in having more radial ribs; *C. tegulata* has only 10–12 ribs. The four worn valves from Isla de Malpelo are a little more elliptical and elongate than the material from the Islas Galápagos and might come to be regarded as another species when more material becomes available.

Carditella marieta new species
(Figures 33, 34)

Description: Shell trapezoidal, longer posteriorly; anterior end sharply rounded; posterior end broad, flared. Prodissoconch small, set off by raised rim, with fine radial sculpture and flattened tip. Lunule and escutcheon narrow. Sculpture of 11–13 strong radial ribs, largest and with wider interspaces posteriorly; radial ribs with scattered nodes. Surface with few brown flecks on white background, especially on posterior slope. Right valve with broad anterior cardinal; resilifer separated from sunken external ligament by low ridge that is swollen dorsally into minute tooth; anterior end with triangular lateral tooth on submarginal ridge, separated from shell margin by groove for margin of left valve; posterior valve margin raised distally into lateral tooth. Left valve with narrow anterior cardinal, which fits above anterior cardinal of right valve; narrow ridge defines anterior border



Figures 29–34. *Carditella* species. **29–32.** *Carditella galapagana* new species, paratypes, external view of left valve, internal views of left and right valves, close-up view of hinge of left valve, Isla Wolf, Islas Galápagos, Ecuador, 274 m, LACM 2931, locality 34-964, lengths = 2.4 mm (external view), 2.4 mm (internal views). **33, 34.** *Carditella marieta* new species, holotype, external view of left valve and internal view of right valve, Islas Marietas, Nayarit, Mexico, CAS 159057, length = 1.6 mm.

[illegible] resilifer separated from sunken external ligament by low ridge; anterior lateral on hinge margin, posterior [illegible] with lateral on submarginal ridge separated from shell margin by groove for margin of right valve. Length to 3.0 mm (Isla San Juanito, Kaiser Collection).

Type Material: CAS 159057, holotype, pair, length 1.6 mm, height 1.2 mm (Figures 33, 34); CAS 12343, paratypes, 1 broken right valve, 9 closed pairs, mostly small, all formerly Stanford University 52426, Dwyer Expedition 1965, from type locality, diving.

Type Locality: Islas Marietas, Bahía de Banderas, Nayarit, Mexico, 20.7° N.

Distribution: Islas Tres Marías, Nayarit, 21.7° N, to

Islas Revillagigedos, Mexico, 18.3° N; approximately 7–46 m (mean = 20.7 m; n = 7).

Other Material Examined: Mexico: Kaiser Collection, Roca Blanca, Isla San Juanito, Islas Tres Marías, Nayarit, 21.7° N, 8–11 m, 6 pairs; Kaiser Collection, Isla María Magdalena, Islas Tres Marías, Nayarit, 21.5° N, 15–23 m, 1 closed pair; CAS 42335, Isla María Magdalena, Islas Tres Marías, Nayarit, 21.5° N, depth not recorded, 1 closed pair; LACM 65-12.41, E anchorage, Isla María Cleofas, Islas Tres Marías, Nayarit, 21.4° N, 5–9 m, 18 pairs, all but one tightly sealed; Kaiser Collection, Isla María Cleofas, Islas Tres Marías, Nayarit, 21.3° N, 16–23 m, 6 sealed pairs; Kaiser Collection, S side, Isla Grande, Islas Marietas, Bahía de Banderas, 20.7° N, 27–40 m, 2 small pairs; CAS 42343, type lot, Islas Marietas, Bahía de Banderas, Nayarit, 20.7° N, "diving"; Kaiser Collection, Majahuitas, Bahía de Banderas, Nayarit, 20.5° N, 6–15 m, 1 small pair; LACM 34-260.6, Bahía Sulphur, Isla Clarion, Islas Revillagigedos, 18.3° N, 46 m, 1 valve.

Etymology: The specific name is derived from the Islas Marietas, the type locality.

Discussion: This species differs from *Carditella galapagana* in that it has a much longer posterior end and fewer ribs, and it is somewhat smaller. This species is similar in shape to *Condylocardia kaiserae* except that, unlike the latter, it has a small sunken external ligament. It is also similar in shape to some juvenile carditids, such as *Cardites laticostata* (G. B. Sowerby I, in Broderip and G. B. Sowerby I, 1833: 195), but can be distinguished by its central resilifer, its larger prodissoconch with a raised rim and radial sculpture, and its wider, less scabrose ribs.

NOTES ON THE SOUTHERN SOUTH AMERICAN SPECIES OF *CARDITELLA*

There are at least five poorly known species of *Carditella* that occur on the southern coast of South America:

Carditella exulata E. A. Smith, 1885 (215; pl. 15, figure 6, 6a). Estrecho de Magallanes, Chile; also Tristan da Cunha and Falkland Islands, South Atlantic Ocean. This species is longer posteriorly and is most similar to *C. naviformis*. It has 14 ribs and attains 4 mm in length. See also Dell (1964: 193, 188, figure 3.6).

Carditella naviformis (Reeve, 1843) (pl. 9, figure 45; 1844: 194; as *Cardita*). Arica, Tarapacá Province, to the Estrecho de Magallanes, Chile. This species is longer posteriorly, has 9–10 ribs, and attains 4 mm in length. See also Dell (1964: 194, 188, figure 3.1).

Carditella pallida E. A. Smith, 1881 (p. 43; pl. 5, figures 9, 9b). Estrecho de Magallanes, Chile. The type species of the genus, it is approximately equilateral, has 14–15 ribs, and attains 5.2 mm in length.

Carditella semen (Reeve, 1843) (pl. 9, figure 43; 1844: 193–194, as *Cardita*) [possible synonyms: *Cardita australis* Philippi, 1858 (23–24; *non Venericardia australis* Lamarck, 1818: 610); *Actinobulus philippii* Tryon, 1872 (254; *nom. nov. pro* "*Cardita australis* Philippi (not Quoy)"); *Cardium parvulum* Dunker, 1861 (36–37; *non* Donovan, 1800; pl. 32, figure 3)]. Pisco, Ica Department, Peru, to Arica, Tarapacá Province, Chile. This species is oval, longer posteriorly, has 14–15 ribs, and attains 3 mm in length.

Carditella tegulata (Reeve, 1843) (pl. 9, figure 48; 1844: 194; as *Cardita*) [possible synonym: *Cardium pygmaeum* Philippi, 1860 (176; pl. 7, figure 3a-c; misspelled as "*C. pygmae*" by Bernard, 1983: 34)]. Islas Lobos de Afuera, Lambayeque Province, Perú (6.9° S) (LACM 38-111.4), to the Estrecho de Magallanes, Chile. Larger specimens are longer posteriorly, have 10–12 ribs, and attain about 4 mm in length. Reeve figured such a specimen, whereas Dell (1964: 194, 188, figure 3.8) illustrated a syntype that is almost equilateral, presumably a smaller specimen. See also Marincovich (1973: 10, figure 9) and Reid and Osorio (2000: 136–139, fig. 7K).

Cardita pacteliana Clessin (1888, p. 20; pl. 6, figures 7, 8), described from Iquique, Chile, was synonymized by F. R. Bernard (1983: 34) with *Carditella naviformis* (Reeve, 1843). However, its original measurement (14 mm) is too large to make this plausible, and it might instead be a small specimen of *Cyclocardia spurca* (G. B. Sowerby I, in Broderip and G. B. Sowerby I, 1833: 195, as *Cardita*), described from the same locality and which Clessin's figure more closely resembles.

DISCUSSION

According to Middelfart (personal communication, December 2002), who has studied the extensive Australian fauna of condylocardiids, only *Condylocardia elongata*, *C. kaiserae*, and *C. koolsae* match the hinge morphology of the type species of *Condylocardia*, whereas the others are closer to the hinge morphology of *Condylocuna*, though differing in sculpture and prodissoconch shape. Moreover, *Condylocardia kaiserae*, with its very long posterior end, is unlike other species of the genus. Eventually, specialists in this group may wish to propose additional generic taxa to accommodate some of these species.

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Prophysaon dubium Cockerell, 1890, the papillose taildropper (Gastropoda: Arionidae): distribution and anatomy

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ABSTRACT

Geographic distributions of many species of native forest slugs in western North America are poorly known. We report on two new records of *Prophysaon dubium* Cockerell, 1890, from the Rocky Mountains in northern Idaho. These records represent a disjunct population from the remainder of the species range in the Cascade Mountains and along the Pacific coast of northwestern North America, and the easternmost distribution records for the species. The genitalia of the dissected specimens from Idaho were similar to previous illustrations of specimens from Oregon and California and to dissected specimens from Oregon and Washington. We believe that the gross anatomy of the genitalia is sufficiently similar to warrant the treatment of the specimens from all areas as a single species. However, the possibility that the geographically disjunct populations represent cryptic species cannot be ruled out without further study.

INTRODUCTION

The genus *Prophysaon* Bland and Binney, 1873, consists of nine recognized species of arionid slugs endemic to northwestern North America (Turgeon et al., 1998). The genus occurs along the Pacific Coast of North America from southeastern Alaska to northern California, east to the Rocky Mountains in northern Idaho and western Montana (Pilsbry, 1948; P. Hendricks, pers. comm.); the portion of the range in the Rocky Mountains is disjunct from the remaining range farther west. *Prophysaon andersoni* (J. G. Cooper, 1872) and *P. humile* Cockerell, 1890, are the only two members of the genus that have been reported to occur in the Rocky Mountains (Smith, 1943; Pilsbry, 1948; Frest and Johannes, 2000).

Prophysaon dubium Cockerell, 1890, is a diminutive (< 20 mm in length when extended) and poorly known slug that is reported to range along the Pacific Coast from northwestern Washington south to northern California (Pilsbry, 1948; Roth and Pressley, 1983; Burke et al., 2000). We report here on an undocumented disjunct population of *P. dubium* from the Rocky Mountains in northern Idaho, and provide descriptions of the distal genitalia of specimens from the states of Washington, Oregon, and Idaho.

MATERIALS AND METHODS

We searched for terrestrial gastropods on and under woody debris and within leaf litter on the forest floor in a wide range of forested habitats in Washington State, Oregon, and Idaho. We found *Prophysaon dubium* at 10 localities in Washington State, one in Oregon, and two in northern Idaho; Jim Baugh provided us with specimens from two additional localities in Washington State (Appendix 1).

Seventeen specimens from Washington State (records 1–3 and 5–12 in Appendix 1), two specimens from Oregon (record 13 in Appendix 1) and three from Idaho (record 14 in Appendix 1) were dissected in the current study. Prior to dissection the specimens were photographed live, subsequently drowned in water, and then preserved in 70% ethanol. Our description of the external appearance was based on the examination of live specimens. The external appearance and the genitalia of the specimens were examined under 7.5–60× magnification with a stereo-zoom microscope. The genitalia of specimens from Thurston County, Washington (record 1 in Appendix 1) and Kootenai County, Idaho (record 14 in Appendix 1) were drawn using camera lucida. Additional specimens were preserved in 100% ethanol for use in future genetic studies. Dissected specimens have been deposited in the collection at the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, USA; one specimen has been deposited at the Delaware Museum of Natural History (DM), Wilmington, Delaware, USA.

RESULTS

DISTRIBUTION AND HABITAT

In Idaho, we found *P. dubium* at two sites approximately 30 km apart. At the site in Kootenai County (record 14 in Appendix 1) all eight specimens were within an approximately 100 m × 10 m area along the base of a steep, north-facing slope abutting the floodplain of Beauty Creek. Most individuals (six of eight) were found along the edge of a grassy clearing adjacent to a western hemlock (*Tsuga heterophylla*)-dominated forest; the two

Figure 1. *Prophysaon dubium* from Beauty Creek, Kootenai County, Idaho (top) and Woodard Bay Natural Resource Conservation Area Thurston County, Washington (bottom). Scale bar = 5mm.

remaining individuals were on a talus slope beneath closed forest canopy. One individual was on a moss-covered rock, six were under woody debris, and one was on a cardboard sheet placed on the ground to attract gastropods. At the site in Benewah County (record 15 in Appendix 1), the only specimen was found on the underside of a well-decayed birch (*Betula papyrifera*) log adjacent to Chatcolet Lake.

At low-elevation sites in Washington and Oregon, specimens were found in mixed forest, consisting of Douglas-fir (*Pseudotsuga douglasii*) or western hemlock (*Tsuga heterophylla*) and bigleaf maple (*Acer macrophyllum*), with abundant sword ferns (*Polystichum munitum*) in the understory; specimens also were found at three high-elevation sites, consisting of mountain hemlock (*Tsuga mertensiana*)-dominated forest with sparse Douglas maple (*Acer glabrum*). Specimens were found either under woody debris (16 of 44 specimens) or on fallen bigleaf maple leaves (28 of 44 specimens).

External Appearance and Distal Genitalia

The external appearance of the specimens from Idaho, Washington, and Oregon is consistent with published descriptions (Pilsbry, 1948; Roth and Pressley, 1983; Kelley et al., 1999) (Figure 1). The background color of specimens includes various shades of brown, reddish-brown, olive, and gray. The mantle is always mottled to some degree with brown or gray pigment, which on some specimens merges to form dark stripes. The foot and to a much lesser extent the mantle are marked by light-brown, orange, copper, and/or gold flecking. The pneumostome is positioned immediately anterior of mid-mantle on the right side. The integument of both the mantle and foot is covered with numerous cone-shaped papillae. Dorsally the foot has a network of dark, longitudinal lines associated with grooves, which, laterally, run obliquely downward to the sole margin. A line of abscission is present on the foot approximately one-fifth of the animal's extended body length anterior of the posterior end.

Internally, the specimens from Idaho, Oregon, and Washington are similar as well. Specimens from Oregon and Washington display both within and between-site variability in the shape and size of the ejaculatory (distal) portion of the epiphallus. The shape of the distal epiphallus varies from oblong to circular. Each of the three specimens from Idaho displays a sausage-shaped distal epiphallus (Figure 2). None of the specimens examined for this study had an ejaculatory epiphallus that exceeded 2 mm in length and in most individuals the length was barely 1 mm. Shared characteristics among specimens from all three states include a broad and elongated vagina (or free oviduct), a long, slender, and convoluted epiphallus leading up to the distal ejaculatory portion, and a small hairpin-shaped penial loop consisting of a short, slender connecting duct and a slightly thicker-walled penis, which in turn inserts on the atrium. The spermatheca (=bursa copulatrix) and spermathecal duct are similarly proportioned in specimens from all areas, but the length of the duct varied from individual to individual. The small ovotestis consisted of approximately 15–30 lobules, each of which was tipped with black pigment.

DISCUSSION

Distribution

Previously, *P. dubium* was known from the eastern slopes of the Cascade Mountains to the Olympic Mountains in Washington, and south to northwestern California (Cockerell, 1890; Pilsbry, 1948; Branson and Branson, 1984; Roth and Pressley, 1983; Kelley et al., 1999; McGraw et al., 2002). Our records from Idaho extend the range of the species westward to the Rocky Mountains (Figure 3). Between the Pacific coastal and Rocky Mountain distributions lies the Columbia Basin, an arid shrub-steppe province in the rain shadow of the Cascade Range (Franklin and Dyrness, 1988; Brunsfeld et al., 2001); this area is unsuitable for gastropods that require mesic forest habitats. Consequently, the Rocky Mountain distribution of *P. dubium* appears to be disjunct from Pacific coastal populations, a distributional pattern shared with numerous plants, animals, and fungi (Slater and Slipp, 1940a, b; Kozloff, 1958; Briggs, 1971, 1974; Shear, 1976; Enghoff, 1985, Barnosky et al., 1987; John-

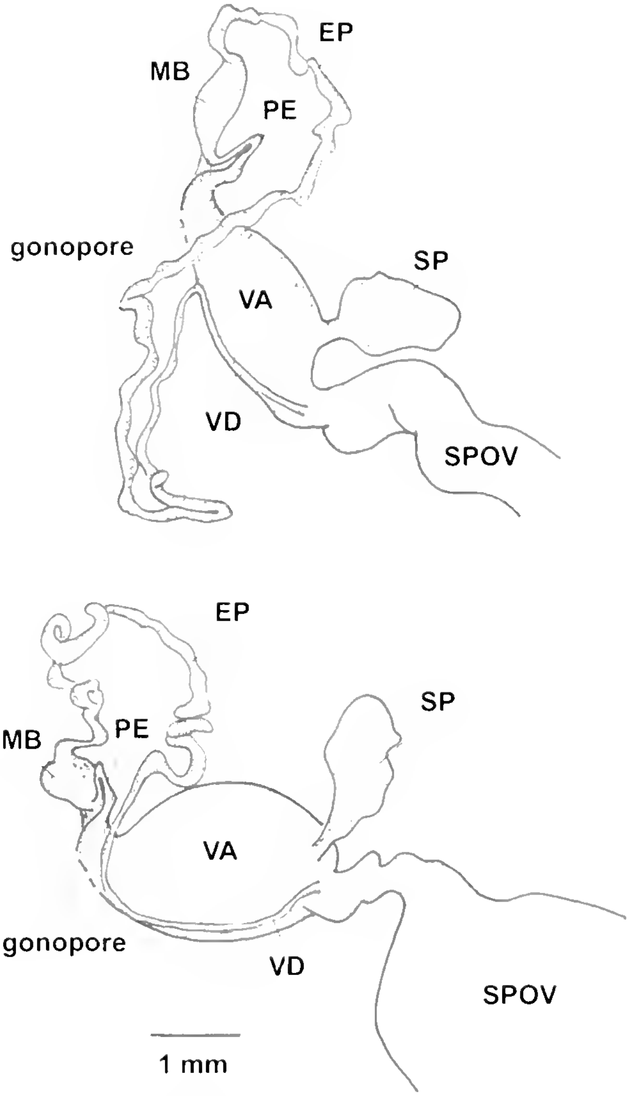

Figure 2. Genitalia of *Prophysaon dubium* from Beauty Creek, Kootenai County, Idaho (upper) (CM 64153) and Woodard Bay Natural Resource Conservation Area, Thurston County, Washington (lower) (CM 64150). EP, epiphallus; MB, Muscular body of epiphallus; PE, penis; SP, spermatheca; SPOV, spermoviduct; VD, vas deferens; VA, vagina.

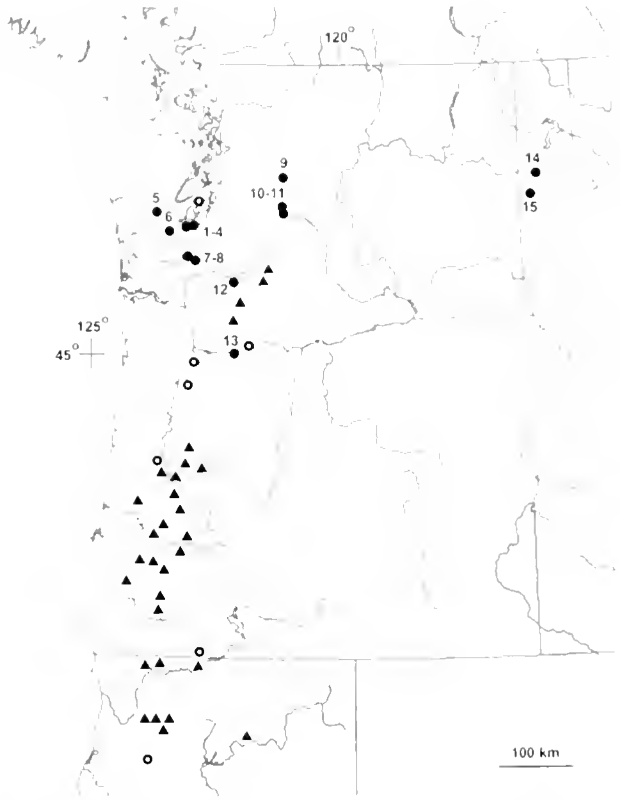

Figure 3. Distribution of *Prophysaon dubium*. Closed circles = specimens examined by us; open circles = records from literature (Cockerell, 1890; Pilsbry, 1948; Branson and Branson, 1984); triangles = records that have been reported to us by regional experts (John Applegarth, Steve Dolan, Nancy Duncan, Tom Kogut, and Barry Roth).

son, 1987; Lorain, 1988; Fender and McKey-Fender, 1990; Shelley, 1993, 1994a, b, c; Wilson and Larsen, 1999; Brunsfeld et al., 2001; Nielson et al., 2001). Varying patterns of differentiation, up to species level, have been documented to accompany this spatial disjunction in different organisms (Brunsfeld et al. [2001] and references cited therein).

DISTAL GENITALIA

All specimens that we examined have a very large vagina that is proportionally broader than shown by Pilsbry (1948) for Oregon specimens. Moreover, the epiphallus is approximately the same length as the specimen, not twice its length as reported by Pilsbry (1948); our findings are consistent with those of Roth and Pressley (1983) for a specimen from California.

The genitalia of the three specimens from Idaho are similar to those illustrated by Roth and Pressley (1983). The ejaculatory portion of the epiphallus of these specimens is sausage-shaped and similar, but much smaller proportionally, to that of the specimen from Oregon pictured by Pilsbry (1948). None of our specimens from Idaho, Oregon, or Washington have an ejaculatory portion that exceeded 2 mm in length, which is in sharp contrast with the illustration in Pilsbry (1948, p. 694, fig. 379), in which this structure is shown to be about 5 mm in length.

Some of the specimens from Washington have a small, spheroid (or egg-shaped) ejaculatory portion of the epiphallus, different from the same structure pictured by both Pilsbry (1948) and Roth and Pressley (1983). Interestingly, the ejaculatory portion of the epiphallus of these Washington specimens is similar in shape and proportions to that drawn by Pilsbry (1948, p. 693, fig. 378) for *P. coeruleum*. Consequently, these Washington specimens easily could be mistaken for *P. coeruleum* were it not for the distinctive external characters of *P. dubium*.

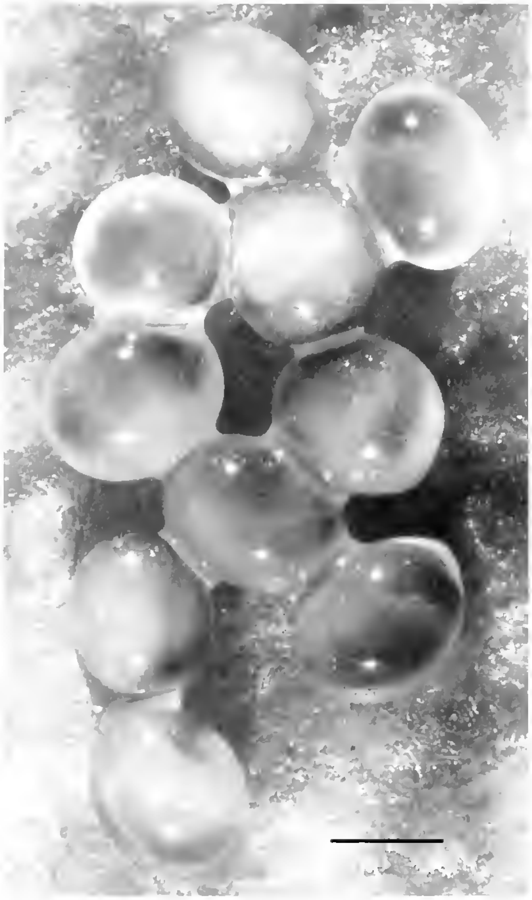

Figure 4. A cluster of eggs of *Prophysaon dubium* photographed on 9 March 2003, approximately four days before hatching. The parent (record 12 in Appendix 1) was collected on 13 December 2002 and eggs were deposited in the laboratory on 15 December 2003. Scale bar = 1 mm.

such as papillose integument and dark markings on the mantle.

Our description of the features of the genitalia of specimens from Washington represents the mature condition, because the specimen from Woodard Bay (record 1 in Appendix 1) deposited a cluster of 11 eggs (approximately 1.3 × 1.2 mm diameter shortly after being laid) in the laboratory on 22 January 2002. Moreover, specimens from Kraus Ridge (record 5 in Appendix 1) laid clusters of 6 and 11 eggs (mean egg size = 2.1 × 1.5 mm, SD = 0.2 for both the length and width, n = 9) (Figure 4) in the laboratory on 15 December 2003. Although no eggs were obtained from the Idaho specimens, their comparably developed genitalia lead us to believe that these animals were sexually mature as well.

TAXONOMIC STATUS

The external appearance and gross anatomy of the reproductive system, which showed only minor individual differences, suggest that our specimens from Idaho, Oregon, and Washington belong to the same species, *Prophysaon dubium*. Until molecular studies clarify relationships we suggest that both the coastal populations and the disjunct Idaho populations of *P. dubium* should be treated as a single species. We cannot explain the discrepancies between the description of distal genitalia by Pilsbry (1948) and our own observations on 22 dissected specimens from three states, including specimens from the type locality and from a site near one of Pilsbry's sites in northern Oregon.

Additional field studies are required to establish the distribution and relative abundance of *P. dubium* in the Rocky Mountains. Moreover, a range-wide genetics study would provide important information on the degree of differentiation between the Idaho and Pacific coastal populations, and will be crucial to the development of an appropriate conservation strategy for these populations.

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APPENDIX 1

Specimens of *Prophysaon dubium* examined for this study.

Washington

1. Woodard Bay Natural Resource Conservation Area, Thurston County; elevation 15 m above sea level (asl); 47° 8.06′ N, 122° 51.04′ W, 17 December 2001, 2 March 2003 (1 specimen, collected by R. Shoal, and J. Ziegltrum; 1 specimen 13 mm extended length while in movement, collected by W. Leonard): CM 64150, CM64983.
2. Priest Point Park, Olympia, Thurston County, elevation 20 m asl; 47° 04.55′ N, 122° 53.80′ W, 5 January 2003 (1 specimen 16 mm extended length while in movement, collected by W. Leonard): CM64977.
3. Woodland Creek, St. Martin's College, Thurston County; 58 m asl; 47° 02.50′ N, 122° 48.17′ W, 11 November 2002, and 2 December 2002 (9 specimens collected by W. Leonard): CM64978.
4. Tolmie State Park, Thurston County; 10 m asl; 47° 07.08′N, 122° 46.62′W, 9 February 2003 (1 specimen 13 mm extended length while in movement, collected by W. Leonard): CM 64876.
5. Schafer State Park, Mason County; 50 m asl; 47

05.85′ N, 123° 27.37′ W; 3 January 2003 (11 specimens ranging between 10 and 15 mm extended length [mean = 12.5 mm] while in movement, collected by W. Leonard and C. Richart): CM64979

6. Headwaters of Porter Creek, Capitol Forest, Thurston County; elevation 350 m asl; 47° 01.33′ N, 123° 07.92′ W; 20 January 2001 (3 specimens, collected by W. Leonard): DM 221684.
7. 0.6 km west of Onalaska post office, Lewis County; elevation 75 m asl; 46° 34.55′ N, 122° 43.53′ W; 9 January 2002 (1 specimen, collected by W. Leonard): CM 64149.
8. Centralia, Lewis County; elevation 60 m asl; 46° 43.3′ N, 122° 56.62′ W; 5 January 2003 (4 specimens ranging between 11 and 18 mm extended length [mean = 14 mm] while in movement, collected by C. Richart): CM64980.
9. South side of State Route 2, 3.2 km west of Stevens Pass summit, Mt. Baker–Snoqualmie National Forest, King County; elevation 1100 m asl; 47° 44.62′ N, 121° 7.20′ W; 7 May 2001, 27 September 2001 (2 specimens, collected by W. Leonard): DM221686, CM 64154.
10. Toll Creek, Wenatchee National Forest (Interstate 90 site #30), Kittitas County; elevation 747 m asl; 47° 17.63′ N, 121° 17.13′ W; 2 July 2001 (1 specimen, collected by J. Baugh, maintained in captivity until October 2002): CM 64151.
11. Kendall Peaks Lakes, Wenatchee National Forest, Kittitas County; elevation 1340 m asl; 47° 25.93′ N, 121° 22.69′ W; 31 July 2001 (1 specimen, collected by J. Baugh, maintained in captivity until October 2002): CM 64152.

12 Kraus Ridge, Gifford Pinchot National Forest, Lewis County; elevation 400 m asl; 46° 26.70′ N, 121° 57.83′ W; 13 December 2002 (4 specimens, collected by T. Burke and W. Leonard): CM64981.

Oregon

13. Ainsworth State Park Campground, Multnomah County; 70 m asl; 45° 35.88′ N, 122° 02.58′ W; 14 December 2002 (3 specimens, collected by W. Leonard): CM64982.

Idaho

14. Beauty Creek at Caribou Ridge Trailhead, Idaho Panhandle National Forest, Kootenai County; elevation 640 m asl; 47° 36.35′ N, 116° 40.15′ W; 21 April 2002 (8 specimens, collected by J. Baugh, T. Burke, and W. Leonard): CM 64153.
15. Heyburn State Park, Benewah County; elevation 650 m asl; 47° 21.13′ N, 116° 46.68′ W; 15 September 2002 (1 juvenile specimen, collected by T. Burke and W. Leonard) (specimen used for genetic studies; photographs in personal collection of WL).

Erratum

In the article by Pastorino (2003: 16) the synonymy of *Amalda josecarlosi* should read:

Ancillaria Tankervillei Swainson.—Dall, 1890: 310.
Ancillaria dimidiata Sowerby.—Strebel, 1908: 25, pl. 1, figs. 2a–e.
Ancilla dimidiata (Sowerby).—Smith, 1915: 96, *non* Sowerby, 1859; *nec* Sowerby, 1892; Marcus and Marcus, 1968, figs. 1–9 (anatomy); Rios, 1970: 102, pl. 32; 1975: 111, pl. 33, fig. 472; 1985: 111, pl. 38, fig. 491; 1994: 143, pl. 46, fig. 613; Figueiras and Sicardi, 1973: 264, pl. 15, fig. 193; Scarabino, 1977: 191, pl. 3, fig. 8; Calvo, 1987: 164, fig. 148.
Ancilla tankervillei Swainson.—Fernández, 1965, figs. 1–4; Castellanos, 1970: 121, pl. 9, fig. 7, *non* Swainson, 1825.

LITERATURE CITED

Pastorino, G. 2003. A new species of Ancillariinae (Gastropoda: Olividae) from the southwestern Atlantic Ocean. The Nautilus 117: 15–22.

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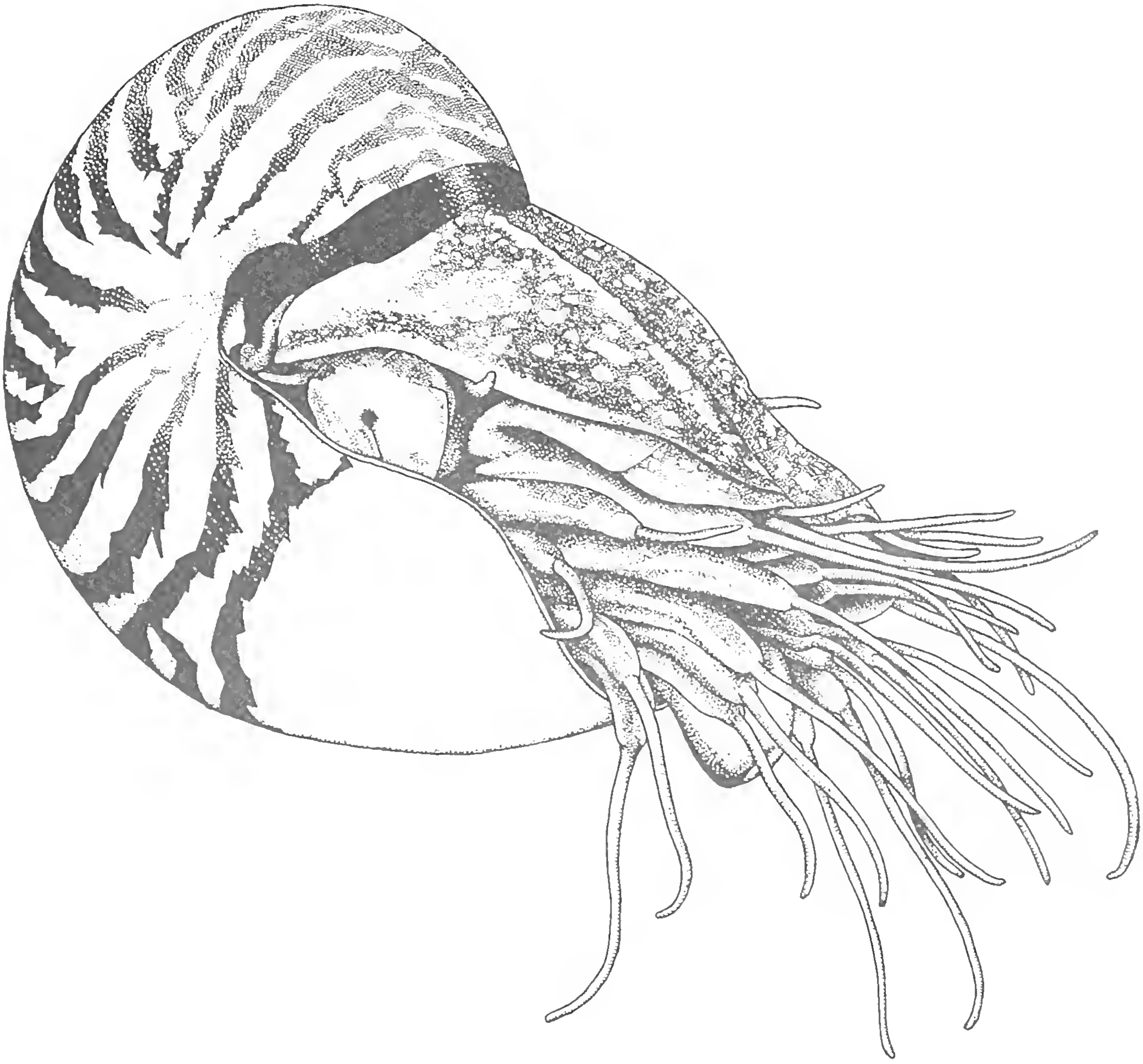

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CONTENTS

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Pseudococculina rimula, a new species (Cocculiniformia: Pseudococculinidae) from off southeastern Brazil

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ABSTRACT

Pseudococculina rimula, new species, is described. It occurs off the state of Rio de Janeiro, in southeastern Brazil, at 350–400 m depth. This is the fist report of the genus in the Atlantic Ocean. The main diagnostic characters of the new species are: shell high, lacking radial sculpture; snout flat, somewhat involved by oral lappets; posterior odontophore cartilages connected to anterior one in median line; gonad connected to posterior end of pallial cavity by a gonoduct running transversally and dorsally in visceral mass; sperm duct mostly closed (tubular), prostate located inside right tentacle; sperm duct opening in a subterminal papilla.

Additional keywords: Anatomy, southwestern Atlantic, Rio de Janeiro.

INTRODUCTION

The Cocculiniformia encompasses taxa with an enigmatic set of primitive and derivate features. Its closest groups are yet to be determined, and it is still questionable whether the taxon is monophyletic. They are usually minute, patelliform gastropods living in the deep sea.

Two papers have been published dealing with cocculiniform gastropods found in deep waters off Brazil: Simone (1996) described an addisoniid, and Leal and Simone (2000) named a pseudococculinid. Both papers provided anatomical information, which is vital for understanding the systematics of the group. Further data on western Atlantic cocculiniformians have been provided by McLean and Harasewych (1995) and Leal and Harasewych (1999).

The present paper provides the description of a third Brazilian species, which was collected by an otter trawl off the coast of São Paulo State, in southeastern Brazil.

MATERIALS AND METHODS

The specimens were dissected using standard techniques, under a stereomicroscope and immersed in fixative. The hard structures (radula and shell) were also examined in a SEM in the Laboratório de Microscopia Eletrônica do MZSP, also using traditional techniques. All drawings were made with the aid of a camera lucida. Abbreviations used in the figures are: **an**, anus; **ap**, aperture of gonoduct; **au**, auricle; **bm**, buccal mass; **br**, subradular membrane; **bs**, blood sinus; **ce**, cerebral ganglion; **cv**, ctenidial vein; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal fold of buccal mass; **dg**, digestive gland, **di**, diaphragm-like septum separating buccal mass from visceral mass; **ef**, esophageal folds; **ep**, epipodium; **es**, esophagus; **et**, epipodial tentacle; **fs**, foot sole; **ft**, foot; **gb**, gonoduct; **gi**, gill, **go**, gonad; **he**, head; **hm**, head muscle; **in**, intestine; **jw**, jaw; **kl**, left kidney; **kr**, right kidney; **m1–m8**, extrinsic and intrinsic odontophore muscles; **mb**, mantle edge; **mc**, mouth sphincter; **mf**, mantle fold; **mj**, jaws, buccal, and oral tube muscles; **mo**, mouth; **oc**, anterior odontophore cartilage; **od**, odontophore; **ol**, oral lappet; **oy**, ovary; **pc**, pericardium; **po**, posterior odontophore cartilage; **pp**, papilla of copulatory tentacle; **pt**, prostate; **pu**, pedal ganglion; **ra**, radula; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sc**, subradular cartilage; **sd**, sperm duct; **se**, chamber originating esophagus and separating odontophore in buccal mass; **sm**, shell muscle; **sn**, snout; **st**, stomach; **te**, cephalic tentacle; **tg**, integument; **tp**, copulatory right cephalic tentacle; **ts**, testis; **ve**, ventricle; **vm**, visceral mass.

Institutional abbreviations used are: MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

SYSTEMATICS

Genus *Pseudococculina* Schepman, 1908

Type species: *Pseudococculina rugosoplicata* Schepman, 1908) by subsequent designation (Wenz, 1938, p. 150).

Pseudococculina rimula new species
(Figures 1–30)

Diagnosis: Shell high, anterior region strongly concave. Sculpture of concentric undulations and threads. Snout flat, surrounded by oral lappets. Jaw plates thin. Posterior odontophore cartilages connected to anterior one along median line. Gonad connected to posterior end of pallial cavity by a gonoduct that runs transversally and dorsally in visceral mass. Sperm duct mostly closed (tubular) opening in a subterminal papilla, prostate inside right tentacle.

Description: Shell (Figures 1–4, 6–10) patelliform, length up to 3 mm, high (height 60–70% of length), white, relatively thick. Protoconch (Figures 6, 7) with one whorl, planispiral, coiled towards ventral region, with a papilla-like projection on each side oriented along direction of coiling; outer surface smooth, opaque. Teleoconch opaque, sculpture of strong, commarginal growth lines and threads. Apex high, curved ventrally and posteriorly, situated along median line of shell, closer to posterior region. Anterior region convex, posterior region weakly concave. Inner surface glossy. Muscular scar horseshoe-shaped (concavity anterior) (Figures 9, 10), narrow posteriorly, thick anteriorly; anterior ends curved toward dorsal and posterior regions.

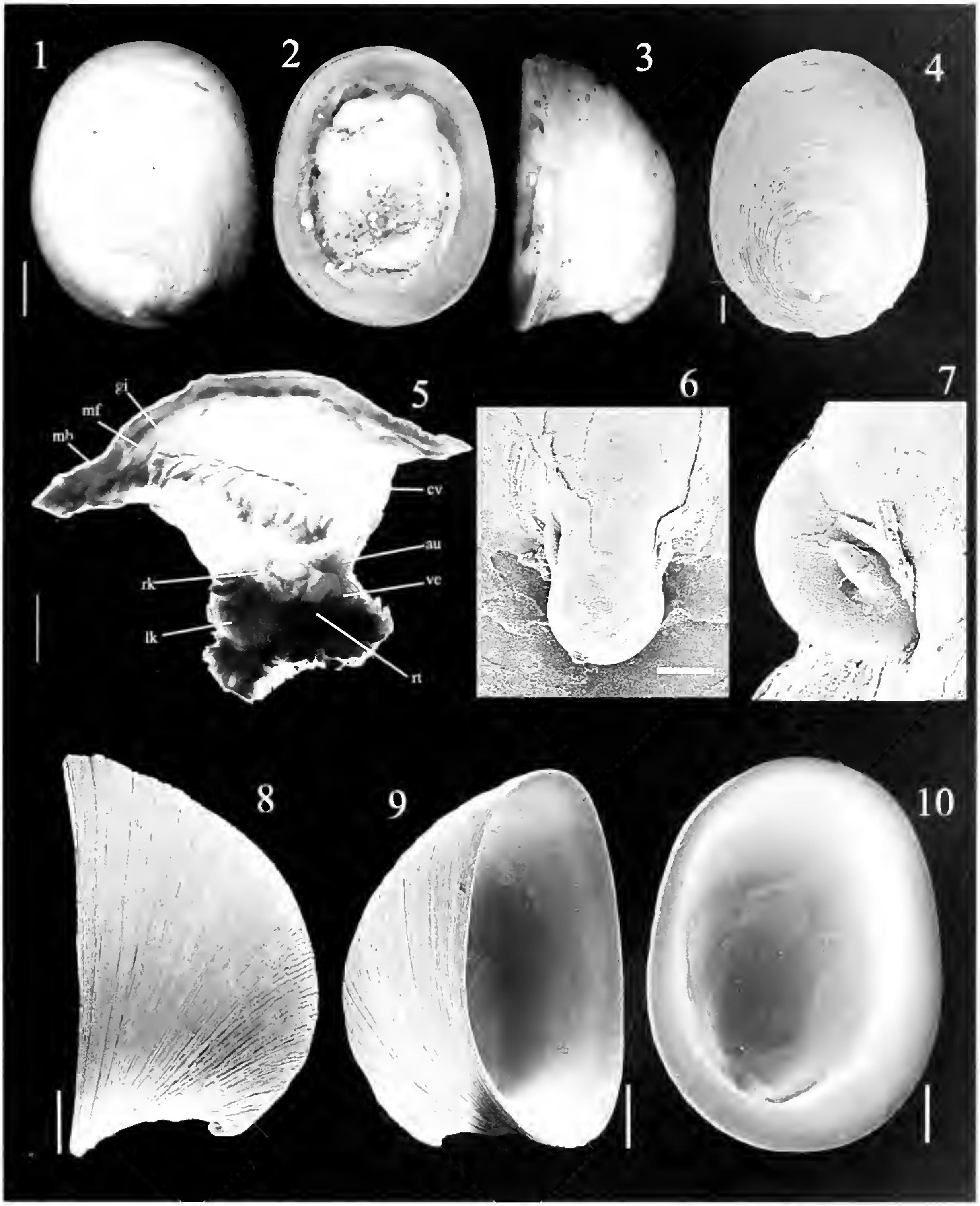
Head-foot (*Figures 2, 14–18*): Head protruded, occupying about 1/3 of total volume of head-foot. Snout well developed, somewhat flat, edges broad, flat, extending externally (Figures 14–17). Oral lappets (lateral expansions on snout) large, covering most of anterior half of animal body. Cephalic tentacles asymmetrical, right tentacle 50 % larger than left tentacle (Figures 16, 17), acting as copulatory organ (details below). Foot sole, or mesopodium, flat, thick, occupying most of ventral surface (Figures 2, 14); anterior edge with a very narrow and shallow furrow. Epipodium about ¼ of shell width, forming a flat flap, inserted between mesopodium and mantle; free edge with 2 pairs of tentacles on each side, inner tentacles longer and slender, outer tentacles shorter and broader (Figure 18). Shell muscle horseshoe-shaped, posterior region narrow (Figure 15), right half broader and thicker than left half; shell muscle gradually becomes thicker toward anterior region; on posterior region of head, shell muscle turns abruptly, first in dorsal, then in posterior direction. Paired head muscles originate as continuations of the antero-dorsal end of shell muscle (Figure 15), right muscle slightly flatter and broader than left muscle, both run toward mid-anterior region immersed in tegument, forming a V-shaped structure; both muscles attach, spreading out, into median region of head wall (Figure 20).

Mantle Organs (*Figures 5, 16, 17, 19*): Pallial cavity shallow, shorter than 1/3 of animal length. Mantle edge simple, weakly bilobed. Gill relatively small, with about 15–20 filaments, left end close to inner edge of left branch of shell muscle; gill narrows gradually towards right, curving posteriorly, running between mantle and right branch of outer edge of shell muscle, up to about mid-length of animal. Gill filaments low, triangular, rod narrow, located in anterior edge. Ctenidial vein contouring anterior part of gill edge. Low and long glandular fold present left half of gill and mantle edge. Rectum and pericardial structures located in posterior region of roof of pallial cavity, just posterior to gill, as described below.

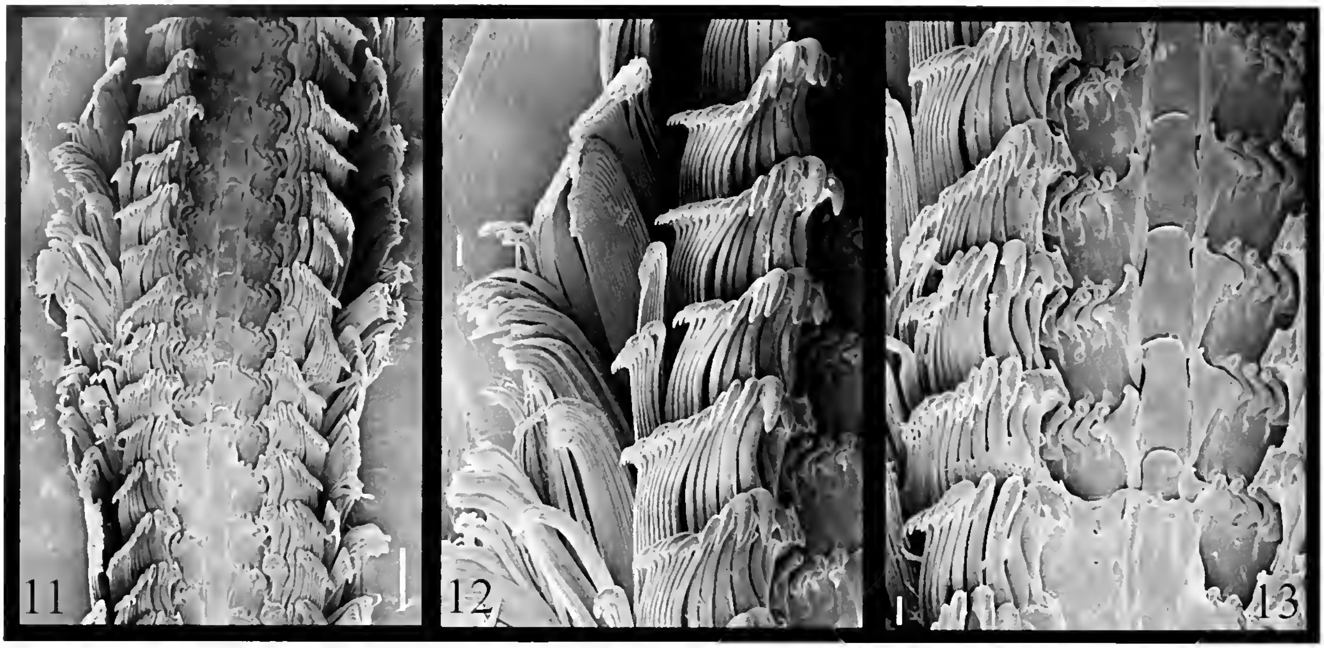
Visceral Mass (*Figure 15*): Compressed ventrally by foot and shell muscle. Stomach occupying central region, surrounded by digestive gland and intestine. Gonad located in postero-ventral region, between two intestinal loops. Digestive gland pale-brown, with small spots forming a net-like mosaic. Gonad cream-colored. A thin diaphragm-like membrane separates buccal mass from remaining posterior structures (Figure 20, di); this membrane inserted in haemocoel surrounding buccal mass; only esophagus, anterior aorta and visceral nerves pass through membrane.

Circulatory and Excretory Systems (*Figures 5, 15, 19*): Pericardium and both kidneys flattened dorso-ventrally, situated in roof of pallial cavity, between gill and posterior end of this cavity. Pericardium broad, about twice heart area, located between left end of gill and left branch of shell muscle. Auricle triangular, its right side attached to pericardium cavity, contouring gill end with a concavity; insertion of ctenidial vein somewhat broad in its anterior region; connection with ventricle narrow, posterior. Ventricle small and thick, muscular, located posterior to auricle, close to rectum. Aorta very small, posterior and at left from ventricle. Left, anterior kidney elliptical, flattened, solid; located between gill posterior region and rectum, touching this latter. Right, posterior kidney, longer and narrower, situated on other side of rectum at same level of left kidney, extending little beyond it toward right.

Digestive System (*Figures 20–30*): Mouth a transversal slit located on antero-ventral region of snout (Figures 14, 20). Buccal sphincter (Figure 23, mc) well-developed and thick. Buccal mass very large, about half of haemocoel length. Oral tube very short, broad, walls thick, muscular; inner surface with low transversal folds. Buccal mass V-shaped, odontophore and esophagus representing respectively ventral and dorsal branches. Inner surface of dorsal wall of buccal mass with pair of broad dorsal folds (Figure 28) that unite anteriorly, edges higher in their mid-region. Dorsal chamber (dc) (delimited by both dorsal folds) relatively deep and broad; inner surface smooth. Jaw plates very thin, color pale brown, anterior end rounded, situated just anterior to connection of dorsal folds (Figures 21, 23, 28); posterior end inconspicuous, gradually weaker in posterior direction up to posterior level of odontophore insertion. Odonto-



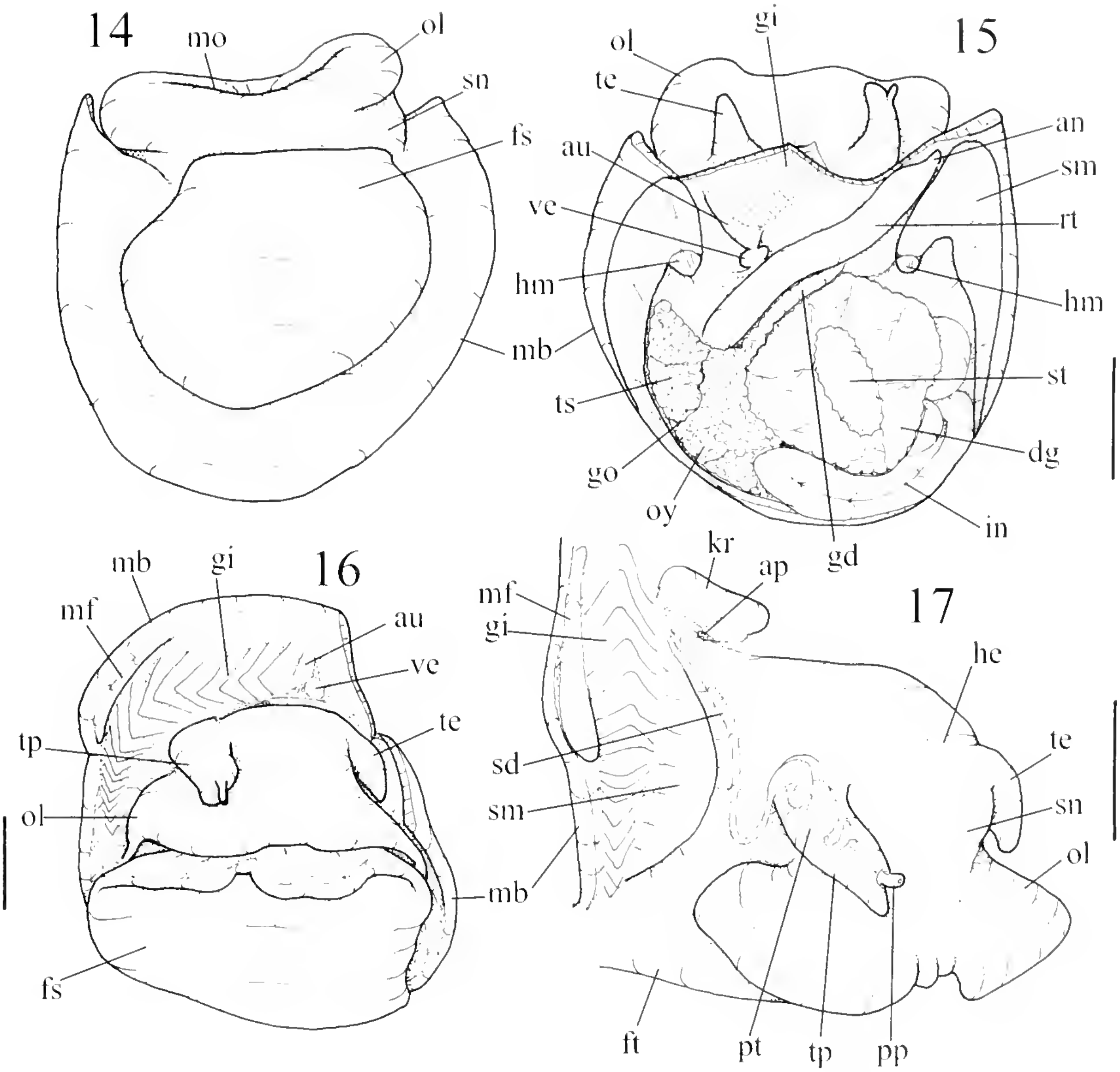
Figures 1–10. *Pseudococculina rimula* new species. **1–3.** Dorsal, ventral, and lateral (left) views of holotype prior to extraction of specimen from shell. Scale bar = 0.50 mm. **4.** Paratype, young specimen, SEM, dorsal view, scale bar = 0.20 mm. **5.** Roof of pallial cavity and adjacent portion of pericardial structures, ventral view, light micrography, carmine stain. Scale bar = 0.25 mm. **6.** Protoconch, SEM, dorsal view. Scale bar = 0.05 mm. **7.** Same, lateral (right side) view, scale bar = 0.02 mm. **8–10.** Paratype adult specimen, SEM, lateral (left side), oblique (right), and ventral views. Scale bar = 0.50 mm.



Figures 11–13. *Pseudococculina rimula* new species. SEM of radular teeth. Scale bars = 50, 10, and 10 μm respectively.

phore pear-shaped, occupying most of buccal mass volume. Odontophore muscles (Figures 23–30): **m1**, series of small and thin muscles connecting buccal mass to adjacent inner surface of haemocoel, more concentrated around mouth; **m1a**, pair of narrow jugal muscles, originating in antero-ventral region of inner surface of snout, running in postero-dorsal direction and inserted in ventral-posterior region of odontophore on lateral region of posterior cartilages; **mj**, pair of muscles moving oral tube and jaws, originating in mid-ventral region of odontophore, contouring anterior edge of posterior cartilages, running toward anterior region, insertion spread out between oral tube and dorsal wall of buccal mass; **m3**, single transversal muscle, very thin, located just ventral to origin of esophagus in buccal mass, uniting both sides of postero-dorsal surface of odontophore; **m4**, large pair of dorsal tensor muscles of subradular membrane, originating in latero-ventral surfaces of anterior cartilages, running toward dorsal region, surrounding these cartilages and covering most of their surfaces, inserting along subradular membrane in its exposed (functional) region; a short portion also originates from posterior cartilages, in their latero-ventral surfaces; **m5**, pair of ventral tensor muscles of radula, originating in posterior edge of posterior cartilage, running toward meso-dorsal region, contouring posterior edge of anterior cartilage, inserting in ventral surface of radular ribbon in posterior half of its exposed region; **m5**, a continuation of **m4**; **m6**, horizontal muscle, single, thin, uniting both anterior cartilages along their inner ventral edges; **m8**, pair of approximator muscles of cartilages, connects anterior and posterior pairs of cartilages, originating from relatively large areas of ventral surface of anterior cartilages, inserting in anterior and inner edge of posterior cartilage; **m11a**, pair of narrow ventral tensor muscles of radula, originating in median corner of posterior cartilages, running toward anterior region on ventral surface of odontophore close to its median line, inserting in ventral end of subradular membrane. Other odontophore non-muscular structures: **oc**, anterior pair of cartilages, elliptical, flat, soft, slightly shorter than odontophore length, anterior end broadly pointed, posterior end blunt; **po**, posterior pair of cartilages, length about ¼ of anterior cartilages, somewhat circular, flat, outer surface convex, inner surface concave, covering postero-external surface of anterior cartilages; both pairs of cartilages fused with each other along their median corner (Figure 29); **br**, subradular membrane, included in radular sac and extending beyond it, covering exposed surface of odontophore within buccal cavity, connecting with lining of oral cavity; **sc**, subradular cartilage, a thin, transparent but strong membrane connected to subradular membrane, covering part of exposed portion of odontophore in buccal cavity (Figure 24). Radular sac with about same length of odontophore, curved in its middle portion, located in middle-right region of visceral mass (Figures 20, 21). Radular nucleus covered by a conspicuous membrane surrounding a blood sinus (Figure 23), located in left-ventral region of visceral mass.

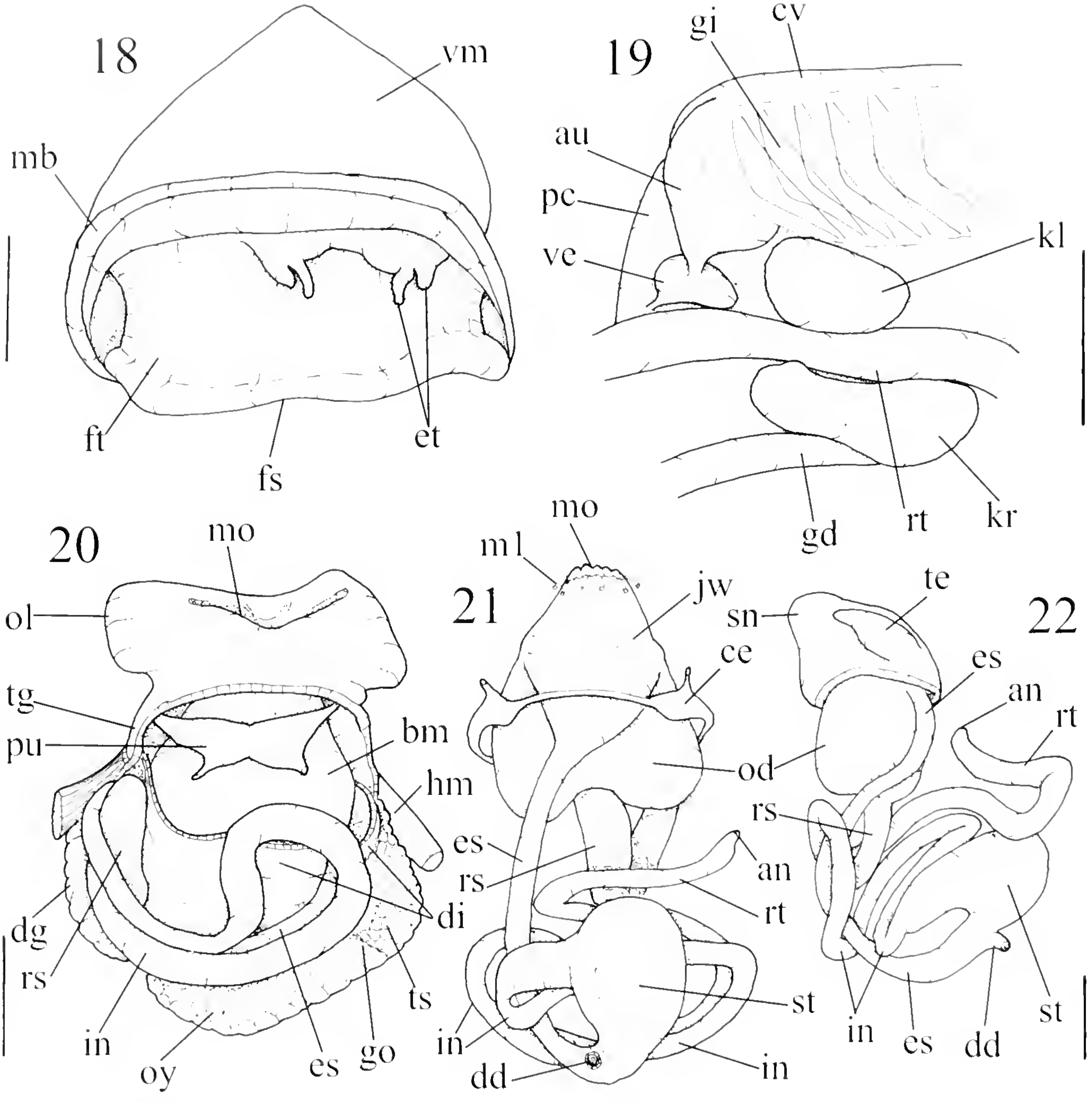
Radula asymmetrical, teeth rows offset by ½ row height; rachidian teeth apparently in level of right half rows. Radular teeth (Figures 11–13): 1) Rachidian antero-posteriorly long, laterally narrow; base flat, with edges slightly elevated; distal cutting edge concave, low, curved inward. 2) Lateral teeth in five pairs: 2a) first lateral tooth triangular, as long as rachidian, base broad, flat, slanted; remaining region narrowing gradually; tip broadly pointed, curved inward; 2b) second, third, and



Figures 14–17. *Pseudococculina rimula* new species, anatomy. **14.** Head-foot and adjacent mantle edge, ventral view. **15.** Whole animal extracted from shell, dorsal view, roof of pallial cavity partially removed. **16.** Whole animal, anterior view, roof of pallial cavity sectioned at on right side then deflected to expose inner structures. **17.** Head and adjacent pallial structures, anterior (but slightly from right side) view, roof of pallial cavity deflected. Scale bars = 0.5 mm.

fourth lateral teeth equal to each other, first tooth slightly smaller, approximately half size of rachidian, situated at same level of broader region of first lateral tooth; base somewhat narrow and short, situated at some distance from adjacent teeth in same row; lateral edge high, curved obliquely, tip sharply pointed, high, curved inward; 2c) outermost lateral tooth as long as rachidian, thick, cylindrical; base narrow, increasing gradually towards distal end; distal end expanding abruptly, with three subterminal, low, inward-turned, stubby cusps located on thicker region; concave region located opposite to cusps, nested in base of corresponding tooth of adjacent row; 3). Marginal teeth in 60–65 pairs, all similar; inner teeth larger, gradually decreasing toward edge of ribbon; larger teeth about 1.5 × rachidian length; base slender and flat, middle region long, rod-like, tall, straight; tip strongly curved inwards, apex sharply pointed, preceded by 6–8 pairs of small, slender, pointed cusps along both sides of broader area of tip.

Origin of esophagus marked by a sudden constriction of dorsal chamber of buccal mass (Figures 21–23). Esophagus narrow, inner surface with pair of low and narrow longitudinal folds (Figure 28), a continuation of dorsal folds of buccal mass. Esophagus runs contouring postero-lateral left surface of odontophore toward postero-ventral region, beyond which it surrounds mid-ven-

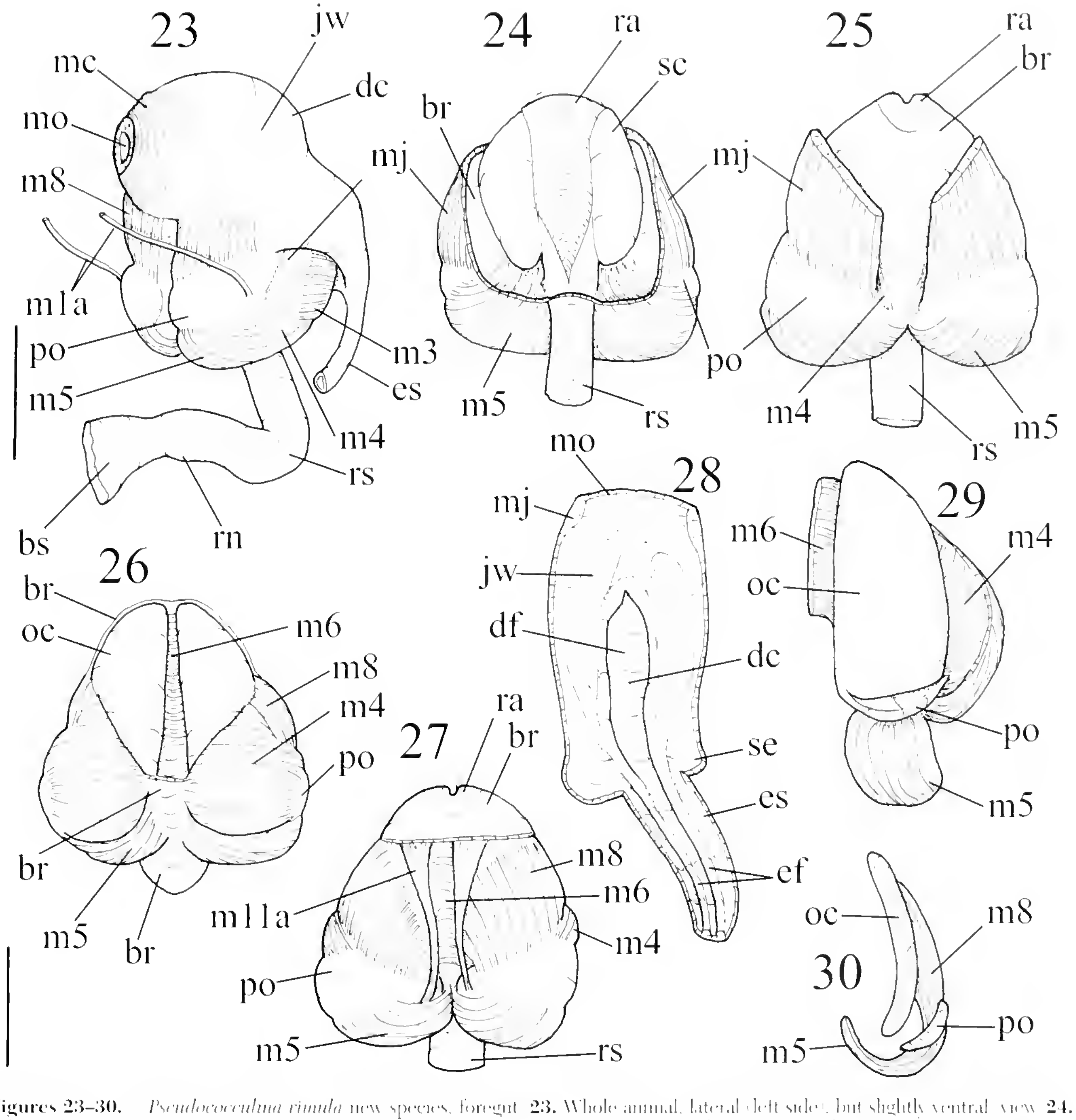


Figures 18–22. *Pseudococculina rimula* new species, anatomy. **18.** Whole animal extracted from shell, posterior view, mantle edge deflected. **19.** Posterior region of pallial roof (dorsal view, depicted by transparency). **20.** Head, ventral view, foot removed, haemocoel exposed with inner structures as *in situ*. **21.** Digestive tube as *in situ* (dorsal view, structures posterior to esophagus slightly deflected). **22.** Same, lateral (left side) view. Scale bars = 0.5 mm.

tral surface of foot along a broad curve; after this esophagus runs toward mid-dorsal region, in direction of shell apex, where it inserts in stomach (Figures 21, 22).

Stomach somewhat narrow and long, located transversally in middle region of visceral mass; its dorsal half broader and spherical (Figures 21, 22), with esophageal connection located in its posterior region. Duct to digestive gland narrow, inserted in left region of esophageal connection. Stomach ventral half flattened and long, narrowing gradually. Inner surface of stomach iridescent, greenish. Digestive gland surrounding stomach for most of its area. Intestinal loops complex, as shown in Figures 21 and 22.

Intestine originates at flattened portion of stomach and is included in mid-ventral region of visceral mass. Intestine is convoluted; after its origin in stomach it runs



Figures 23–30. *Pseudococculina rimula* new species, foregut. **23.** Whole animal, lateral (left side), but slightly ventral view. **24.** Odontophore, dorsal view. **25.** Same, ventral view. **26.** Odontophore, dorsal view, radula and subradular cartilage removed, both anterior cartilages deflected. **27.** Odontophore, ventral view, first layer of muscles and membranes removed. **28.** Dorsal wall of buccal mass and anterior esophagus, ventral-inner view. **29.** Odontophore, dorsal view, detail of its right side with most muscles deflected for showing right cartilages. **30.** Same, representation of a transversal section. Scale bars = 0.5 mm.

obliquely toward dorso-lateral region, surrounding ventral surface of stomach; in latero-dorsal right region of visceral mass intestine describes broad curve toward postero-ventral region, runs down to mid-ventral region of visceral mass, touching inner surface of foot and surrounding middle portion of esophagus; in this region intestine curves broadly, returning to its previous location, running parallel to it but in opposite direction; in latero-dorsal right region of visceral mass intestine describes yet another broad loop ventral to the previous loop, turning along horizontal plane toward left; in latero-anterior left region of visceral mass it curves abruptly toward right region, surrounding odontophore; this last loop runs obliquely toward latero-anterior right region of roof of pallial cavity. Anus located on latero-posterior right region of roof of pallial cavity roof (Figure 15).

Reproductive System (Figure 15): Gonad located in latero-posterior left region of visceral mass, just dorsal to shell muscle. Testis more anterior, with smooth, uniform surface. Ovary occupying mid-posterior region of gonad, with granulose surface. Gonad with short projection running along right edge of rectum. Gonad gradually becomes a gonoduct along middle portion of rectum. Gonoduct with thin, transparent walls, running obliquely on surface of visceral mass alongside rectum; opens in pallial cavity posterior end, posterior to right (posterior) kidney (Figures 15, 19). A shallow furrow runs from this aperture, contouring latero-posterior right corner of pallial cavity to aperture of sperm duct (Figure 17). Posterior aperture of sperm duct directed to left, protected by a pair of diverging folds. Sperm duct very narrow, thin-walled, entirely closed (tubular), running along right edge of floor of pallial cavity to an area anterior to right tentacle, where it folds abruptly toward left and penetrates base of right tentacle. Sperm duct runs along right cephalic tentacle, its basal 2/3 intensely coiled and with thick glandular walls, thicker in its middle portion, then gradually narrows, its distal 1/3 very narrow and almost straight (Figure 17). Sperm duct opening in tip of subterminal papilla; papilla cylindrical, short, nested in a small concavity (which may indicate possible ability to retract).

Central Nerve System (Figure 21): Ganglia relatively small and separated from each other. Paired cerebral ganglia relatively distant from each other, located in medially in latero-dorsal region of buccall mass. Pedal ganglia relatively close to each other, situated between middle and anterior portions of ventral surface of buccal mass (Figure 20). Remaining ganglia not studied in details.

Shell Measurements (Length, Width, and Height in mm): MZSP 35349 paratype #1: 3.0 by 2.5 by 1.7; #5: 3.3 by 2.7 by 1.7; #6: 3.4 by 2.6 by 1.9.

Type Material: Holotype MZSP 35348; Paratypes: MZSP 35349, 12 specimens; MNRJ 8965, 3 specimens (1 without shell); MNHN, 3 specimens (1 without shell), all from type locality, otter trawl, C. Magenta leg., Apr. 2002.

Type Locality: Off southern Rio de Janeiro State, Brazil (350–400 m depth), rocky bottom.

Distribution: Know only from type locality.

Habitat: Rocky bottom.

DISCUSSION

The generic allocation of the new species is mainly based on the diagnosis of the genus provided by Marshall (1985: 522) and Haszprunar (1988: tab. 2, p. 177) with addition of further data from other authors (e.g., McLean and Harasewych, 1995). *Pseudococculina rimula* appears to be the first occurrence of the genus in the Atlantic.

Pseudococculina rimula differs from the remaining congener species in having a high shell and by lack of radial sculpture. *Pseudococculina rimula* resembles *P. gregaria* Marshall, 1985, from New Zealand, but differs by having higher shell, narrower radular rachidian, and by different characters of the copulatory right tentacle, such as uncoiled sperm duct and absence of papilla.

The anatomy of the new species fits the general plan described for the family (Haszprunar, 1987, 1988). Anatomical characters defining the family are gonad divided into testis and ovary and right cephalic tentacle as copulatory organ. However, the new species possesses some peculiarities, as, e.g., the apparent absence of salivary glands (glands are sometimes poorly developed in cocculiniform limpets), the ventricle free from the rectum, the presence of a short opened portion in the sperm duct running on pallial floor; and the presence of a visceral gonoduct. The gonoduct has been regarded as a modification of the right kidney, but, if so, it is only part of the kidney underwent modification, since there is a detectable right kidney. The presence of a very long right kidney, in the *P. rimula* gonoduct, is found in the comparable topology of *Yaquinabyssia careyi* McLean, 1988 (Haszprunar, 1988, fig. 2). The muscles of the odontophore differ from those of *Kurilabyssia venezuelensis* (McLean, 1988; Haszprunar, 1988, fig. 3) in lacking oral tube muscle and dorsal retractor of cartilages, and by a greater development of the buccal sphincter, differ from those of *Coccopygya hispida* Marshall, 1986 (Haszprunar, 1987: fig. 3) in lacking buccal dilators and ventral protractors of cartilage, and also by the great development of the buccal sphincter; differ from *Cocculina nipponica* Kuroda and Habe, 1949 (Sasaki, 1998: fig. 70) in lacking the pair of ventral tensor muscles of radular sac, lacking the pair of median protractor muscle of subradular membrane, and in having the pair of posterior cartilages.

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Distribution of the introduced freshwater snail *Melanoides tuberculatus* (Gastropoda: Thiaridae) in Brazil

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ABSTRACT

This article describes the alarming spread and current distribution of the introduced thiarid gastropod *Melanoides tuberculatus* in Brazil. The first record of this species in Brazil was in 1967 in Santos, state of São Paulo, and since then has been recorded, in the states of Ceará, Distrito Federal, Minas Gerais, Paraíba, Rio de Janeiro, Paraná, Santa Catarina, Bahia, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Pará, Pernambuco, Piauí, Rio Grande do Norte and Tocantins. Records concerning the latter ten states are reported for the first time. *M. tuberculatus* has been studied as the intermediate host of some diseases, and is known as displacing native species. The rapid spread of this species, the lack of any control or monitoring, and the scarce knowledge of the Brazilian freshwater mollusks indicate that serious damage to the ecosystem with probable implications to public health are to be expected. Two other detected species of invasive freshwater mollusks in Brazil are the bivalves *Corbicula fluminea* and *Limnoperna fortunei*.

Additional keywords: Invasive, invading, mollusks, Mollusca, South America, Neotropical

INTRODUCTION

Research on introduced species have received special attention in the last few years due both to the increasing number of invasions and to the economic, environmental, and human health problems they have caused throughout the world.

South America has been especially hard hit by invasive freshwater species such as *Corbicula fluminea* (Müller, 1774) (Bivalvia: Corbiculidae), *Limnoperna fortunei* (Dunker, 1857) (Bivalvia: Mytilidae), and *Melanoides tuberculatus* (Müller, 1774) (Gastropoda: Thiaridae). The two first species were introduced into South America respectively in the 1970s and in 1991, probably in ballast water of ships originating from southeastern Asia (Darrigran and Ezcurra de Drago, 2000).

In North America, *C. fluminea* may have caused some populations of native bivalves to decline, but other native populations seem to coexist with it (Strayer, 1999). In Argentina, *L. fortunei* is well established in the Plata Basin and, in addition to altering the diversity of native molluscan communities, its high-density populations are causing economic problems because they restrict water intake and flow through sewage treatment plants, power plants, and industrial facilities (Darrigran, 2002). In Brazil, economic and environmental problems caused by *L. fortunei* occur at least in the municipalities of Guaíba and Viamão, state of Rio Grande do Sul, according to Mansur et al. (2003).

Reports on the introduction the Afro-Asiatic thiarid *M. tuberculatus* in Latin America started in the 1960s and it is now distributed in all countries of this region (Brown, 1994). In this paper the current distribution of this invasive species in Brazil is reported as well as its impact on both human health and the environment. The goal is to provide the first complete report of the distribution of the species, based on field studies (result of several projects), three major malacological collections in Brazil, and the literature. This report shall provide the background for future control and/or monitoring the spread of the species.

MATERIALS AND METHODS

The main source of data is in the institutional collections, which contain voucher material of field projects, mainly those involving the authors. The institutions are: Instituto Oswaldo Cruz, Rio de Janeiro (FIOCRUZ), Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), and Museu de Zoologia da Universidade de São Paulo (MZSP). Additionally, published reports on the occurrence of *M. tuberculatus* were also examined.

Figure 1. Current distribution of the invasive gastropod *Melanoides turbeculatus* in Brazil.

RESULTS

In the Neotropical Region, the first records of *M. tuberculatus* came from Brazil (1967), Cuba (1983), Désirade (1985), Dominica (1975), Grenada (1970), Guadeloupe (1979), Honduras (1980), Martinique (1979), México (1972), Panamá (probably 1971), Peru (1990), Puerto Rico (between 1964 and 1966), Saint Lucia (1978), Venezuela (1972), Argentina-Paraguay (1999) (Abbott, 1973, Amaya-Huerta and Almeyda-Artigas, 1994; Chrosciechowsky, 1973; Larrea et al., 1990, Peso and Quintana, 1999; Pointier, 1993; Pointier and Delay, 1995; Pointier et al., 1989; Vaz et al., 1986).

In Brazil, the first record of *M. tuberculatus* was in Santos, state of São Paulo, in 1967 (Vaz et al., 1986). Subsequently, it has been recorded in the states of Minas Gerais (Silva et al., 1994); Paraíba (Paz et al., 1995); Rio de Janeiro (Thiengo et al., 1998, 2001, 2002a, 2002b; Giovanelli et al., 2001), Ceará (Melo and Cordeiro, 1999), Paraná (Pereira, 2000) and in the Federal District, Brasília (Vaz et al., 1986; Garcez and Martins-Silva, 1997).

In addition to the above-mentioned reports, we searched for additional material of *M. tuberculatus* in Brazil. They are listed below and in represented in Figure 1. State of Pará: Itaituba; Tocantins: São Félix do Tocantins and Peixe; Piauí: Parnaguá; Ceará: Crato; Paraíba: Campina Grande, João Pessoa, Santa Luzia, São Mamede, and Sousa; Pernambuco, Macaparana and São Lourenço da Mata; Rio Grande do Norte: Pendências; Bahia: Cariranha, Coaraci, Itajuípe and Salvador; Federal District: Brasília; Goiás: Barro Alto, Campinorte, Campinaçu, Colinas do Sul, Formosa, Minaçu, Niquelândia, Nova Iguaçu de Goiás, Padre Bernardo, Santa Rita do Novo Destino, Uruaçu and Vila Boa; **Mato Grosso:** Cuiabá, Nobres, Rosário Oeste and Várzea

Grande; **Mato Grosso do Sul:** Miranda and Três Lagoas; **Minas Gerais:** Além Paraíba, Belo Horizonte, Betim, Caeté, Contagem, Corinto, Lagoa Santa, Ouro Branco, Pedro Leopoldo, Prudente de Moraes and Vespasiano; **Espírito Santo:** Cachoeiro de Itapemirim; **Rio de Janeiro:** Angra dos Reis, Areal, Bom Jesus de Itabapoana, Cambuci, Campos, Cantagalo, Cardoso Moreira, Carmo, Duque de Caxias, Engenheiro Paulo de Frontin, Guapimirim, Itaboraí, Itaguaí, Itaocara, Japeri, Magé, Mangaratiba, Maricá, Mendes, Miguel Pereira, Niterói, Paraíba do Sul, Petrópolis, Piraí, Resende, Rio Bonito, Rio de Janeiro, Sapucaia, Saquarema, São Fidelis, São Francisco de Itabapoana, São Gonçalo, Sumidouro, Valença, Vassouras and Volta Redonda; **São Paulo:** Americana, Atibaia, Bariri, Castilho, Colômbia, Eldorado, Florinea, Guariba, Ilha Comprida, Ipauçu, Itapira, Itapura, Mongaguá, Panorama, Paranapanema, Pedro Toledo, Registro, Ribeirão Preto, Santos, Serra Azul, Sertãozinho and Suzanópolis; **Paraná:** Londrina, Sertaneja and Sertanópolis; **Santa Catarina:** Camboriú and Palhoça. Data concerning the States of Bahia, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Pará, Pernambuco, Piauí, Rio Grande do Norte and Tocantins are new.

DISCUSSION

The origin of the introduction of *Melanoides tuberculatus* to Brazil remains unknown, but it is probably linked to the plant and freshwater ornamental fish trade. This route of introduction and spreading of freshwater snails had been previously reported i.e. Cowie (2002), Madsen and Frandsen (1989) and Pointier (1999). The first record of *M. tuberculatus* in the state of São Paulo was in aquarium hobbyist stores in the city of Santos (Vaz et al., 1986). Thiengo et al. (1998) reported its introduction by local fish farmers and rapid colonization in fish tanks in Guapimirim, Rio de Janeiro, probably in the 1970s. In the states of Minas Gerais, Rio de Janeiro and São Paulo, where more extensive surveys have been done, this species has been collected from almost all hydrographic basins, inhabiting lotic, lentic, polluted or clean water environments, often in dense populations. *Melanoides tuberculatus* has since spread from few points in São Paulo to all Brazilian regions in the course of three decades.

The biological and parthenogenetic reproductive characteristics of *M. tuberculatus* make this species a good invader (Pointier and Delay, 1995). Its adaptability to a wide range of environmental conditions and high reproductive capacity has encouraged its use, mainly in the French West Indies, in the biological control of the host snails of *Schistosoma mansoni* Sambon, 1907. Field and laboratory experiments undertaken in Desirade, Guadeloupe, Martinique and Santa Lucia, revealed the ability of this species to limit and even exclude species of *Biomphalaria* in these islands (Pointier, 1993; Pointier et al., 1989, 1991, 1993). In Brazil, studies on the impact of exotic species are scarce: Giovanelli et al. (2001) observed that in Sumidouro, an area of low endemicity for schistosomiasis, *M. tuberculatus* had substantially reduced *Biomphalaria glabrata* (Say, 1818) populations, indicating a process of competitive exclusion; in Betim and Prudente de Moraes, Guimarães et al. (2001) reported marked reduction in populations of *B. glabrata* and *B. straminea* (Dunker, 1848) in two lakes, after the arrival of this thiarid, followed by complete disappearance of the former species eight years later. During the last three years, our group (unpublished data) has been performing a quantitative study of *M. tuberculatus*, *B. straminea* and *Lymnaea columella* Say, 1817 populations in a large reservoir in Minaçu, Goiás. Preliminary data indicated that native populations of the thiarid *Aylacostoma tenuilabris* (Reeve, 1860), previously abundant in the Tocantins River, have been replaced by dense populations of *M. tuberculatus*. Fernandez et al. (2001) documented the displacement and decline of *B. glabrata* and *Pomacea lineata* (Spix, 1827) populations in a small stream on the campus of Fundação Oswaldo Cruz, Rio de Janeiro, after the introduction of *M. tuberculatus*. This data is already sufficient for demonstrating that native species, suffering declines from pollution and destruction of their natural habitats, are now being impacted by *M. tuberculatus*.

Morphological and conchological studies on samples of *M. tuberculatus* from Brazil are being performed in order to detect the occurrence of distinct morphs as observed in the Caribbean islands. Conchological characteristics and spatial distribution provide evidence that morphs of *M. tuberculatus* exist in Martinique and that new morphs of this species develop in rapid succession (Pointier, 1989; Pointier et al., 1993). Recently, Simone (2001) included samples of *M. tuberculatus* in the phylogenetic analyses of Cerithioidea, based on comparative morphology, and has not found any evidence for differentiating morphs.

Regarding medical and veterinary importance, *M. tuberculatus* acts as potential intermediate hosts of *Paragonimus westermani* (Kerbert, 1878), *Clonorchis sinensis* (Cobbold, 1875) and *Centrocestus formosanus* (Nishigori, 1924) helminthes responsible respectively for paragonimiasis, clonorchiasis and centrocestiasis transmission (Amaya-Huerta and Almeyda-Artigas, 1994; Pointier, 1999). Until recently *M. tuberculatus* had never been recorded harboring larval forms of those trematodes in Brazil. A recent report by Boaventura et al. (2002) found specimens from Maricá and Guapimirim shedding Pleurolophocercus cercaria.

We believe that the ability of *M. tuberculatus* to spread rapidly and colonize new, natural and man-made habitats alike, generally resulting in high-density populations, threatens the native mollusc fauna and should be closely monitored and documented.

Considering the lack of substantial taxonomic and ecological studies on our freshwater mollusc fauna and the environmental impact caused by alien species, in spite of extensive areas endemic for schistosomiasis in Brazil, and the possible effectiveness of *M. tuberculatus* as a competitor of planorbid intermediate hosts of *S. mansoni*, expansion of this species must be thoroughly monitored and controlled, which has not been done.

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Horaiclavus sysoevi, a new species (Neogastropoda: Drilliidae) from the northwestern Indian Ocean

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ABSTRACT

Horaiclavus sysoevi, a new gastropod species of the family Drilliidae, is here described from the northwestern Indian Ocean. The new species, consisting of four shells collected during the John Murray Expedition (1933–34), has previously been misidentified in the literature as *Horaiclavus splendidus* (A. Adams, 1867), type species of the genus *Horaiclavus* Oyama, 1954. *Horaiclavus sysoevi* is conchologically similar to *H. splendidus*, but differs in having a bigger size, a shell outline less cylindrical, teleoconch whorls more convex, a smaller number of axial ribs, a higher number of spirals, a narrower and longer siphonal canal. The new species is compared with other members of the genus *Horaiclavus* from the Japan. With this note the geographical distribution of *Horaiclavus* is enlarged.

Additional keywords: Gastropoda, *Horaiclavus splendidus*, Goto Islands, Gulf of Aden

INTRODUCTION

The familial position of the genus *Horaiclavus* Oyama, 1954, is still uncertain, as pointed out by Sysoev (1996) who followed Shuto (1979, 1983) in assigning this genus to the family Drilliidae Morrison, 1966. The type locality of *Horaiclavus splendidus* (A. Adams, 1867), type species of the genus and herein illustrated for comparative purposes, is Goto Islands (Japan). According to Sysoev (1996) *Horaiclavus madurensis* (Shepman, 1913) is conchologically very similar to *H. splendidus* and should be treated as a subspecies. In this paper we describe a new species of *Horaiclavus*, *Horaiclavus sysoevi* new species from the Gulf of Aden. The new species, represented by four shells collected during the John Murray Expedition in 1933–1934, was figured by Sysoev (1996: 2, figs. 20–21) as *H. splendidus*. The holotype of *H. splendidus* is housed in the H. Cuming collection at The Natural History Museum, London; the holotype of *H. sysoevi* is housed in the John Murray Expedition collection, also at The Natural History Museum. Acronyms used in the text are: The Natural History Museum of London (BMNH), John Murray Expedition (JME). Comparison with other known species of the genus *Horaiclavus* is presented. With this report the geographical distribution of *Horaiclavus* is expanded.

SYSTEMATICS

Superfamily Conoidea Rafinesque, 1815
Family Drilliidae Morrison, 1966
Genus *Horaiclavus* Oyama, 1954

Horaiclavus Oyama, 1954, p. 52.

Type Species: *Mangelia splendida* A. Adams, 1867, p. 309, pl. 19, fig. 24, holotype BMNH 1966458.

Description: Shell of medium size for family, slender, fusiform, turriculate with tall spire. Protoconch paucispiral, dome-shaped, smooth, with 1–2.5 convex whorls, bluntly rounded. Teleoconch with 8–9 convex whorls, last whorl ovate. Sculpture of weak axial collabral ribs that extend from suture to suture, crossed by faint spiral lines. Siphonal canal broad and short. Aperture narrow, ovate, and elongate, without distinct sinus on anterior or posterior regions.

Horaiclavus splendidus (A. Adams, 1867)
(Figures 1–3, 6–8)

Description: Shell of medium size, up to 30 mm length, fusiform, spire tall. Protoconch paucispiral, of 1.5 whorls, dome-shaped, about 650–700 µm in maximum diameter, smooth, color light-brown. Transition to teleoconch not well marked. Teleoconch elongate and turriculate, consisting of 8–9 convex whorls, slightly angled on shoulder (8 whorls in the holotype). Sculpture of weak, equally spaced, wavy collabral axial ribs that extend from suture to suture, 11–13 ribs on the earlier whorls, 16–18 on the last whorl. Axial ribs crossed by very faint spirals, 35–45 on last whorl, more evident near

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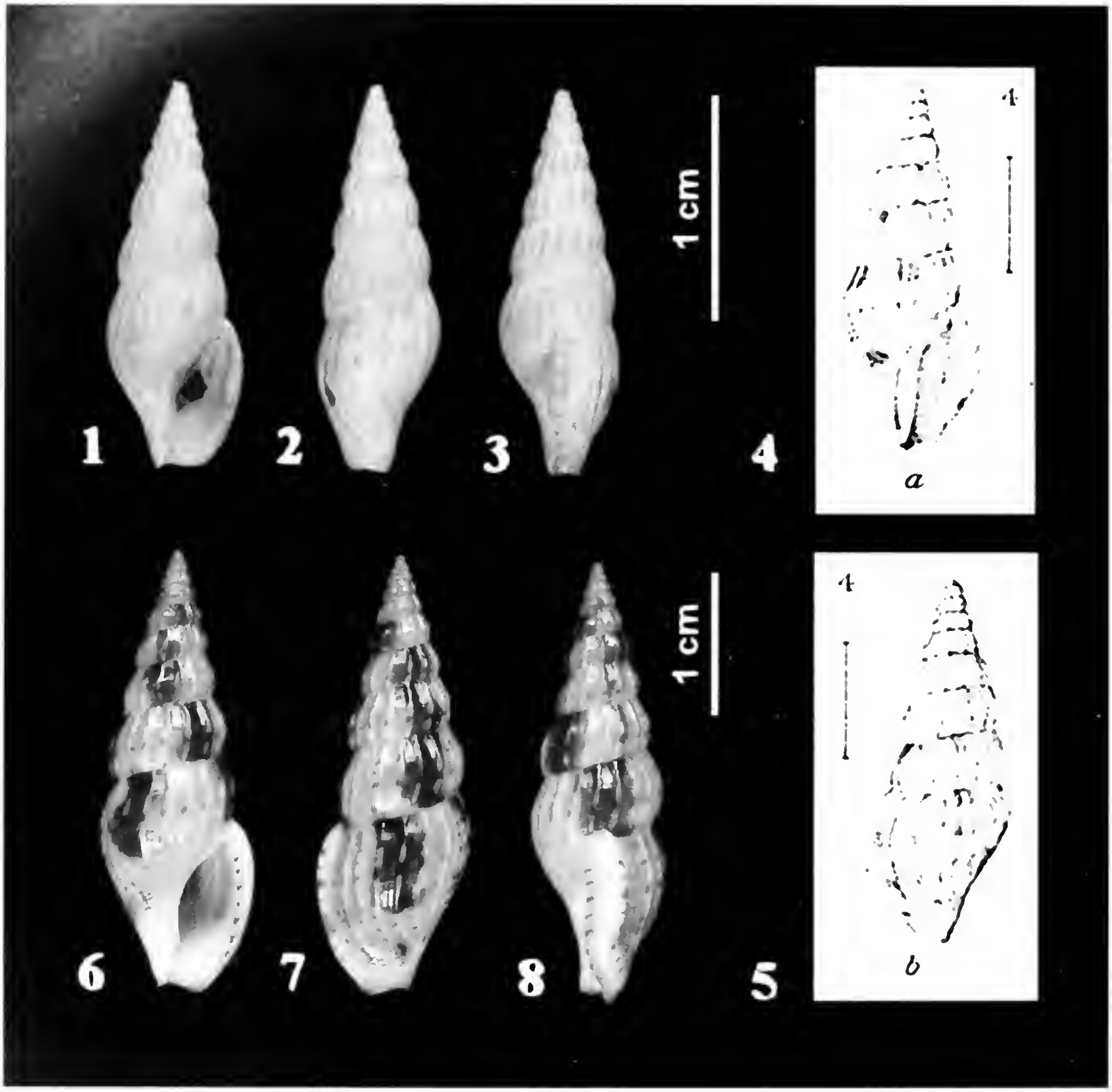
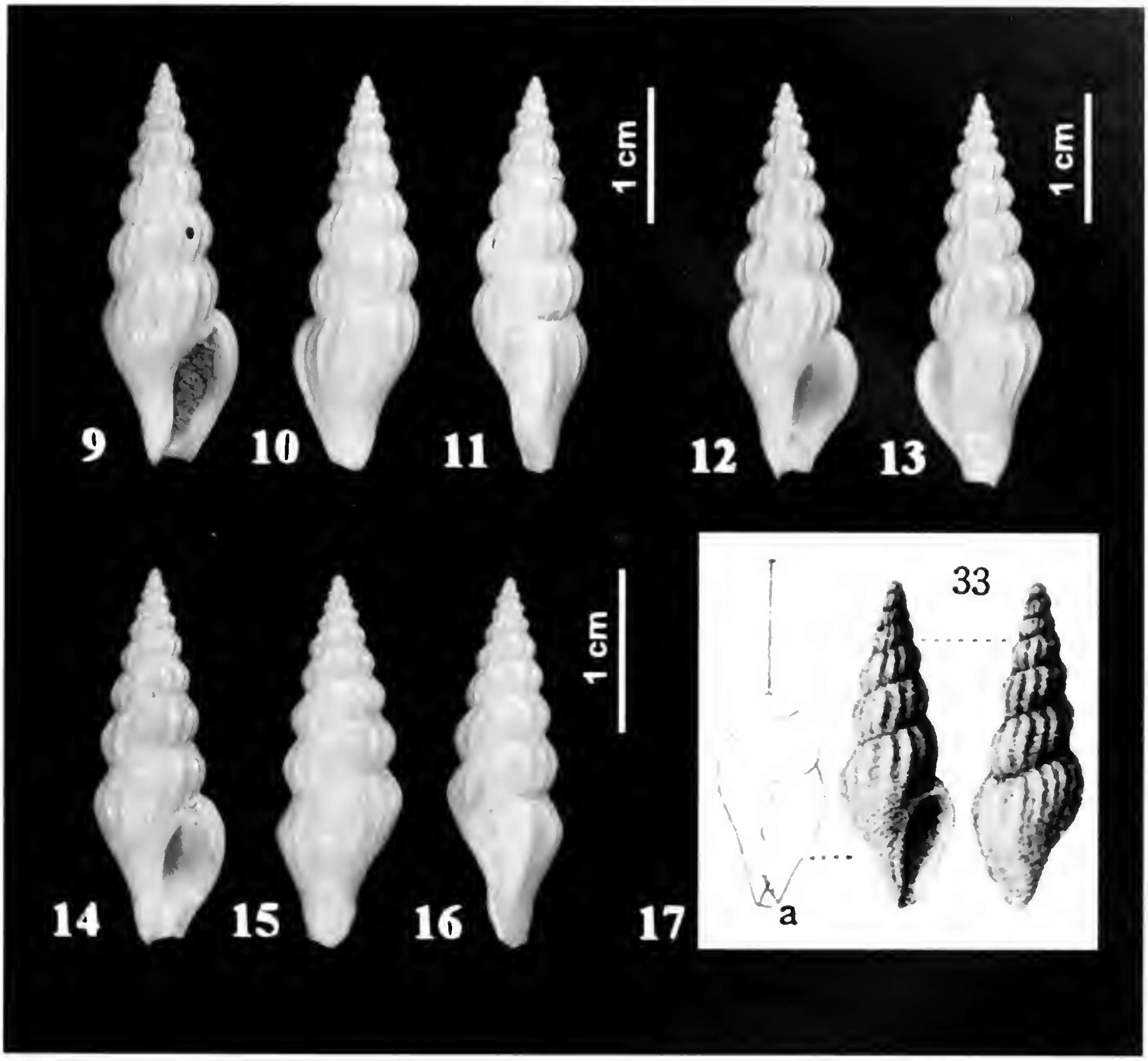


Figures 1–8. *Horaiclavus splendidus* (A. Adams, 1867) and *Horaiclavus madurensis* (Schepman, 1913). **1–3.** *Horaiclavus splendidus*, holotype BMNH 1966458, Goto Islands, Japan, 18.3 × 7.0 mm. Apertural, dorsal, and lateral views. **4–5.** *Horaiclavus madurensis*, original drawing by Schepman (1913, figs. 4a, b). **6–8.** *Horaiclavus splendidus*, dredged in deep water by fishermen, Aliguay Island, Mindanao, Philippines, 29.2 × 6.0 mm. Apertural, dorsal, and lateral views.

base. Suture well defined. Aperture narrow and ovate; anterior or posterior sinuses not distinct, about one third of shell length; inner color white. Siphonal canal short and large. Columella curved, smooth. Outer lip thick, inner surface smooth. Shell color variable; most common pattern of light brownish background with reddish brown flammulate axial stripes and spiral lines of same color. Peristome white with brown-reddish internal dots. Soft parts unknown.

Remarks: *Horaiclavus* was considered in the past as an Indo-Pacific genus. The type species is from Goto Islands (Japan) and the shells from the JME are from the Gulf of Aden (northwestern Indian Ocean). In addition to its broad geographic distribution, this genus seems to have a considerable bathymetric range, at least from 50–732 m, as reported by Kuroda, Habe and Oyama (1971: 212) and Sysoev (1996: 2). As for its systematic position, we agree with Sysoev (1996) who, "until



Figures 9–17. *Horaiclavus sysoevi* new species and *Horaiclavus shitoensis* Oyama, 1954. **9–11.** *Horaiclavus sysoevi* holotype, BMNH 20010405, Gulf of Aden, northwestern Indian Ocean (JME, station 183, 533 m), 32.3 × 11.0 mm. Apertural, dorsal, and lateral views. **12–13.** Paratype B, BMNH 20010404B, Gulf of Aden, northwestern Indian Ocean (JME, station 176, 732 m), 33.0 × 10.5 mm. Apertural and dorsal views. **14–16.** Paratype A, BMNH 20010404A, Gulf of Aden, northwestern Indian Ocean (JME, station 176, 732 m), 28.0 × 9.8 mm. Apertural, dorsal, and lateral views. **17.** *Horaiclavus shitoensis*, original drawing in Oyama (1954: fig. 33–33a).

the examination of the radula", has conservatively followed Shuto (1975, 1983) in assigning *Horaiclavus* to the Drilliidae. *Horaiclavus madurensis* (Schepman, 1913) has been considered by Sysoev (1996) as a subspecies of *H. splendidus*. The original description and figure of *H. madurensis* (Schepman, 1913: fig. 4) strongly corroborate this point of view, with the shell of this latter species being only somewhat broader and shorter than that of *H. splendidus*. For a better comparison of these two taxa, the original drawing of *H. madurensis* is depicted (Figures 4–5).

Horaiclavus sysoevi new species
(Figures 9–16)

Description: Shell of medium size, up to 33 mm length, fusiform, spire tall. Protoconch paucispiral, of 2.5 whorls, dome-shaped, about 450–500 µm in maximum diameter, smooth, color cream. Transition to teleoconch not well marked. Teleoconch elongate and lanceolate, with 8–9 whorls. Sculpture of weak, equally spaced, wavy collabral axial ribs, 10–11 on earlier whorls, 12–15 on last whorl, extending from suture to suture. Spiral lines 55–65, regularly spaced and of about same size, overriding axial ribs on last whorl. Suture well-defined. Aperture narrow and ovate, anterior and posterior sinuses not distinct, about one third of the entire height, inner color cream. Siphonal canal short and narrow. Columella curved, smooth. Outer lip thick, inner surface smooth. Shell color uniformly cream with brownish tinges. Soft parts unknown.

Type Locality: Gulf of Aden, northwestern Indian Ocean, 13°43′18″ N, 47°56′4″ E to 13°16′00″ N, 47°50′42″ E, 533 m, JME (1933–34), HEMS Mabahiss station 188.

Type Material: Holotype, BMNH 20010405, length 32.3 mm, from type locality; Paratypes A–C, BMNH 20010404A–C, Gulf of Aden, northwestern Indian Ocean, 12°04′06″ N, 50°38′36″ E, 732 m, JME (1933–34), HEMS Mabahiss station 176.

Etymology: This species is named in honor of Dr. Alexander V. Sysoev (Zoological Museum of Moscow State University, Russia), recognized scientist who has greatly contributed to the knowledge of the malacology.

Remarks: *Horaiclavus sysoevi* is herein described from four shells collected during the JME (1933–34) that were already reported and in part figured by Sysoev (1996: 2, figs. 20–21) under the name *H. splendidus*. We have been able to examine the holotype of *H. splendidus* from the H. Cuming collection and the four shells from JME. This has led us to unquestionably separate that lot of shells from *H. splendidus*. The new species is similar to *H. splendidus*, but clearly distinguishable by several diagnostic features. *Horaiclavus sysoevi* exhibits: more lanceolate and less cylindrical body shape, bigger size, smaller and higher spired protoconch, more convex teleoconch whorls, small number of axial ribs, higher number of spirals, narrower and longer siphonal canal, different shell color. The new taxon is easily distinguishable from other members of the genus *Horaiclavus*: *H. shitoensis* Oyama, 1954 (p. 21, figs. 33–33a), Kuroda, Habe and Oyama (1971: 213, figs. 12–13), Oyama (1973: 50, fig. 7) and Tsuchida and Kurozumi (1996, 11, fig. 5 (1–3)) is much smaller (about 10 mm length), the teleoconch is less elongate and lanceolate, with only 5–6 whorls, stronger axial ribs and spiral sculpture. We provide the original drawing of *H. shitoensis* for comparison (Figure 17). *Horaiclavus sysoevi* also differs markedly from *H. filicinctus* (Smith, 1882), this latter species being smaller (about 10 mm length), with a teleoconch more biconical and much less elongated, with only 5–6 whorls, stronger and fewer axial ribs, and the aperture about half of shell length, as can be observed in the pictures reported by Kuroda, Habe and Oyama (1971: 213, figs. 19) and Tsuchida and Kurozumi (1996: 11, fig. 8 (5)). These authors figured also another species of *Horaiclavus* (*op. cit.*, p. 11, fig. 8 (6)) that is somewhat similar in size and teleoconch shape to *H. shitoensis* but completely different from *H. sysoevi*. With this note the geographical distribution of *Horaiclavus* is expanded, now ranging from the Japan Sea to the northwestern Indian Ocean.

ACKNOWLEDGMENTS

We would like express our deep gratitude to Ms. Kathie Way, Dr. John Taylor, and Mrs. Joan Pickering (all from BMNH) for kindly forwarding the type material of *Horaiclavus splendidus* and *H. sysoevi* and relevant literature. We are deeply indebted to Dr. Kurozumi (Natural History Museum and Institute, Chiba, Japan) for sending valuable references related to *Horaiclavus* spp. Sincere thanks are due to Dr. Antonio Bonfitto (Laboratorio di Malacologia, Università di Bologna, Italy) and Dr. Paul Callomon (Department of Malacology, Academy of Natural Sciences, Phyladelphia, USA) for help with literature. We also want to thank Dr. Marco Oliverio (Università di Roma "La Sapienza", Italy) for critical comments and advice.

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Description of *Scabrotrophon inspiratum* new species (Gastropoda: Muricidae) from Vanuatu

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ABSTRACT

Scabrotrophon inspiratum new species is described from Vanuatu and compared with *S. scarlatoi* (Golikov and Sirenko, 1992) from the Kurile Islands and with *S. regina* (Houart, 1985) from the Philippine Islands. The three species are illustrated.

Additional keywords: Neogastropoda, Muricoidea, southwest Pacific Ocean.

INTRODUCTION

The muricids collected during the MUSORSTOM 8 cruise to Vanuatu have been enumerated and discussed by Houart (2001). Twenty-six species have been recorded, of which three remained unidentified and two were described as new. The material studied here was already known at that time, however it was then considered as a possible Coralliophilinae by the author. Reconsideration of my previous analysis and comparison with the additional material prompted the description of *Scabrotrophon inspiratum* new species herein. This brings the total number of muricids (excluding Coralliophilinae) collected during the MUSORSTOM 8 cruise to Vanuatu to 27; of these, three still remain unidentified. Text abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris, France; ZISP: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia; dd: dead-collected specimen; lv: live-collected specimen (for other abbreviations see Table 1).

Table 1. Shell morphology abbreviations (after Merle, 1999 and 2001) (see Figures 1 and 2).

SHOULDER	
IP	Infrasutural primary cord (primary cord on shoulder)
CONVEX PART OF TELEOCONCH WHORL AND SIPHONAL CANAL	
P1	Shoulder cord
P2–P6	Primary cords
S1–S4	Secondary cords
S1	Secondary cord between P1 and P2; S2, secondary cord between P2 and P3, etc.
ADP	Adapical siphonal primary cord

SYSTEMATICS

Family Muricidae Rafinesque, 1815
Genus *Scabrotrophon* McLean, 1996

Type species: *Trophon maltzani* Kobelt and Küster, 1878; northeastern Pacific, by original designation.

Remarks: The genus *Scabrotrophon* was introduced to include a few species previously allocated to *Nipponotrophon* Kuroda and Habe, 1971 (Radwin and D'Attilio, 1976; Myers and D'Attilio, 1980; Roth, 1981; Houart, 1985; Tiba and Kosuge, 1985). McLean (1996) originally included five species and nine taxa have been added by Houart and Lan (2001).

Scabrotrophon inspiratum new species
(Figures 1, 3–7)

Description: Shell medium sized for the genus, up to at least 41.9 mm in length at maturity (paratype MNHN), broadly biconical, spinose, lightly built. Protoconch whorls unknown (broken). Spire high, up to 6 broadly convex, shouldered, spinose teleoconch whorls. Shoulder broad. Suture impressed. Sculpture of teleoconch whorls consisting of low, narrow axial lamellae, each with broad, flattened primary spines. Shoulder spine longest. Other axial sculpture of numerous growth striae. First whorl damaged, second and third with 15 lamellae, fourth with 15–18, fifth with 15, last whorl with 13–15 lamellae. Spiral sculpture of high, strong, narrow, primary cords. Convex part of teleoconch whorl with P1 and P2 visible on early whorls; P1 more conspicuous. Last whorl with P1–P4, S4, P5, S5, P6, ADP. P1 and P2 more broadly spaced than P2, P3, and P4. S1 absent in paratype. Primary cords producing long, broad, flat, weakly abaperturally bent spinelike projections at

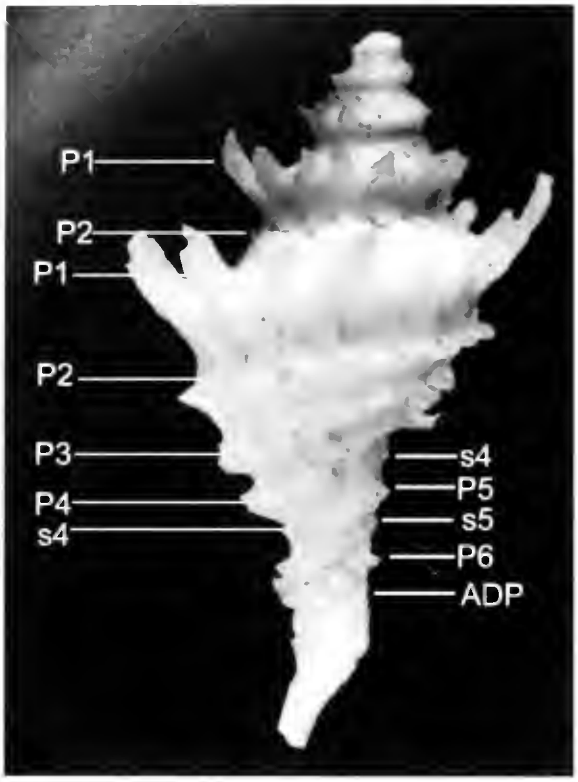

Figure 1. *Scabrotrophon inspiratum* new species, holotype, MNHN. 39.2 mm length (see Table 1).

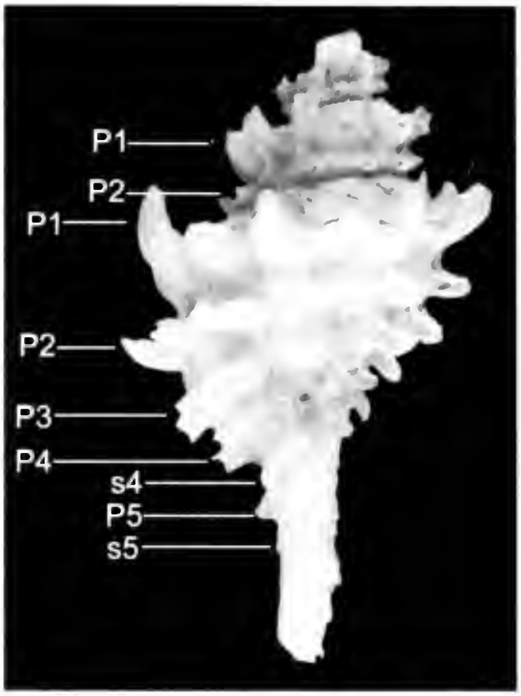

Figure 2. *Scabrotrophon scarlatoi* (Golikov and Sirenko, 1992), holotype, ZISPb n° 57628, 24.7 mm length (see Table 1).

intersection of axial lamellae. Shoulder spines more broadly developed, longest, weakly adapically bent. Spines of P2, P3, and P4 small, almost horizontal on P2, weakly abapically bent on P3 and P4. Presence of small broadly open spinelets on P5, S5, and P6 on abapical portion of siphonal canal. Aperture large, ovate. Columellar lip narrow, smooth, with weak, broad parietal node adapically (holotype), rim broken. Anal notch moderately broad and deep. Outer apertural lip weakly crenulate, thin, smooth within. Siphonal canal long, broad, weakly abaxially bent at tip, open. Shell white. Operculum and radula unknown.

Type Material: Holotype, 39.20 length × 22.70 mm width, and one paratype, both MNHN unnumbered (dd), N.O. Alis, Cruise MUSORSTOM 8, station CP 1110, Bouchet and Richer de Forges coll. 08 Oct. 1994, both from the type locality.

Type Locality: Northeast of Espiritu Santo Island, 1360 m, 14°19′ S, 167°15′ E, Vanuatu, southwestern Pacific Ocean.

Etymology: Latin *inspiratum*, inspired; in connection to the type locality northeast of Espiritu Santo Island.

Remarks: *Scabrotrophon inspiratum* new species differs from *S. scarlatoi* (Golikov and Sirenko, 1992) (Figures 2, 8, 9) from the Kurile Islands in having a more ovate aperture and a broader siphonal canal, narrower and more widely spaced primary cords giving rise to sharp, flat, broad spine-like projections instead of rounded ones in *S. scarlatoi*; P2 is less apparent on early teleoconch whorls in *S. inspiratum* new species; the spines of P1 are less upwardly curved and comparatively longer, while these of P3 and P4 are less downwardly curved in *S. inspiratum* new species. The new species differs from *Scabrotrophon regina* (Houart, 1985) (Figure 10) from the Philippines in having more strongly keeled whorls, a longer siphonal canal, lower spiral cords, and narrower, longer spine-like projections with lower axial lamellae between the spines. Moreover, there is no primary spiral shoulder cord (IP) and no secondary cords (except S4) in *S. inspiratum*, while *S. regina* has a shoulder cord and S2, S3, and S4, respectively between P2 and P3, P3 and P4, P4 and P5. Other species of *Scabrotrophon* are strongly dissimilar and do not need to be compared herein.

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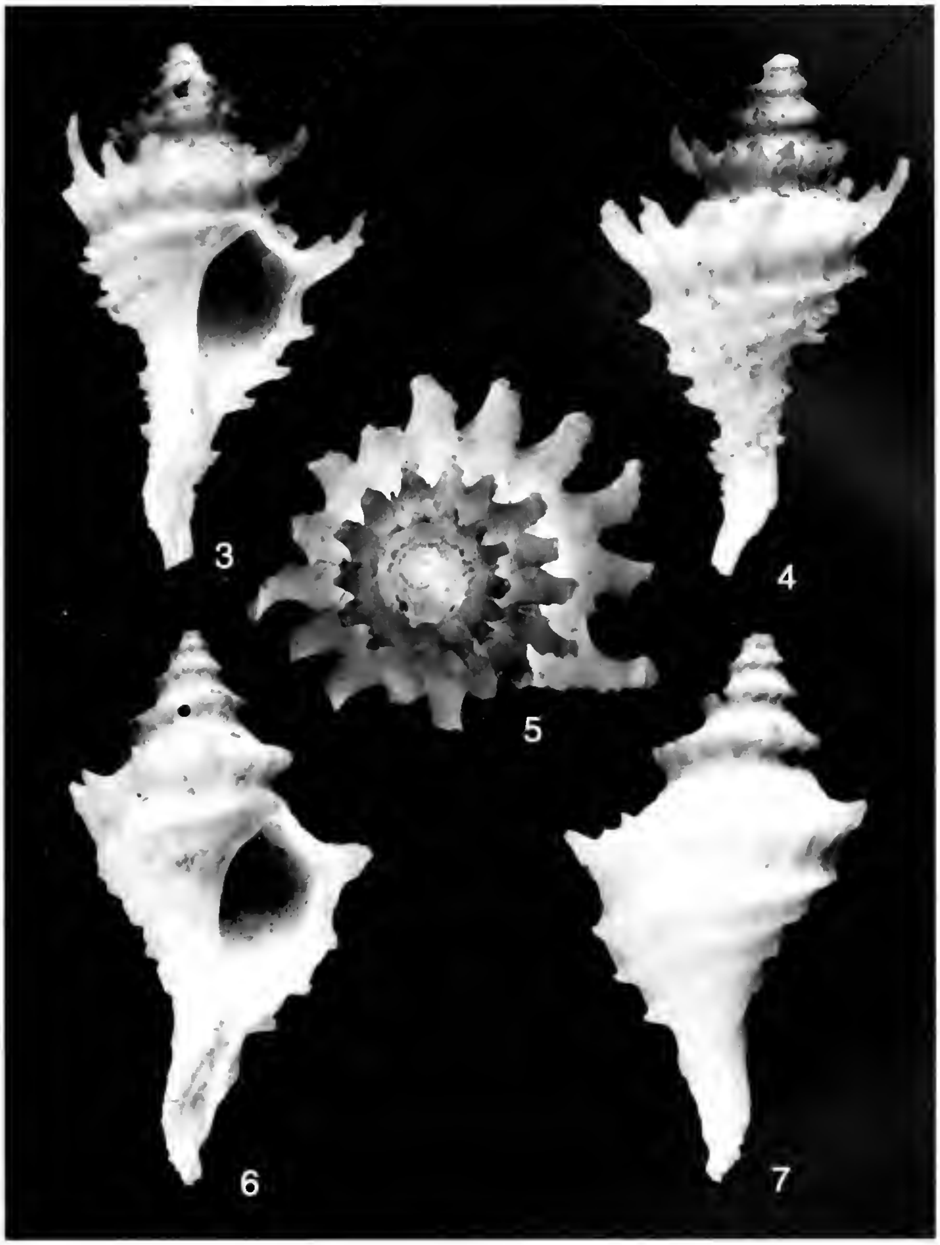
I am most indebted to Philippe Bouchet (Muséum national d'Histoire naturelle, Paris) for giving me the opportunity to study the material collected during the numerous ORSTOM-MNHN expeditions and for reading the manuscript. I am also very grateful to Boris I. Sirenko (Zoological Institute of the Russian Academy of Sciences) for the loan of the holotype of *S. scarlatoi*, to Didier Merle for his comments on spiral sculpture morphology, and to Marco Oliverio (Università di Roma "La



Figures 3–7. *Scabrotrophon* species. **3–7.** *Scabrotrophon inspiratum* new species, Vanuatu, N/O Alis, MUSORSTOM 8, station CP 1110, 14°49′ S, 167°15′ E., 1360 m (dd); **3–5.** Holotype MNHN, 39.2 mm length. **6–7.** Paratype MNHN, 41.9 mm length.

Sapienza", Roma) for having compared the new species with coralliophilids and for his comments.

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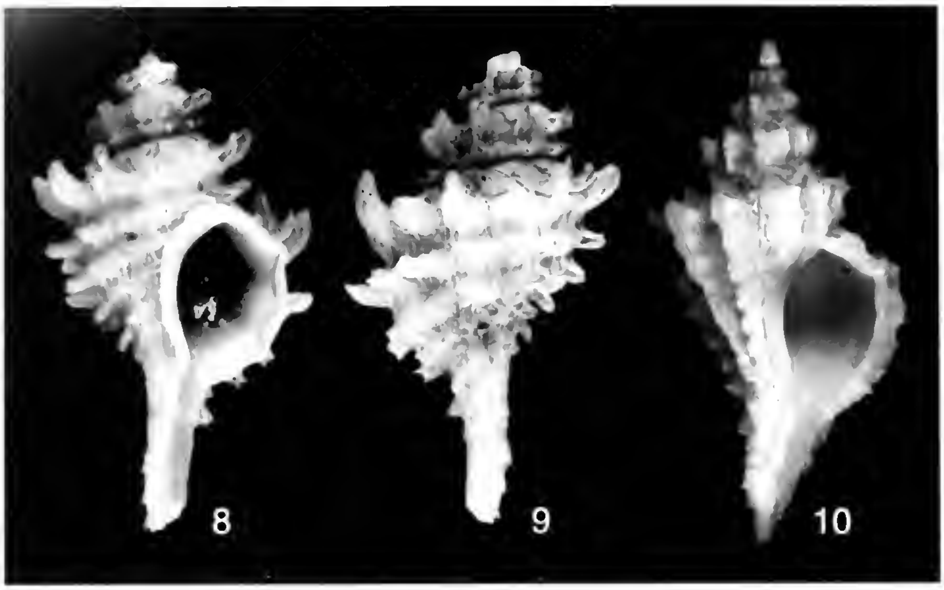

Figures 8–10. *Scabrotrophon* species continued. **8–9.** *Scabrotrophon scarlatoi* (Golikov and Sirenko, 1992), Kurile Islands, eastward from Iturup Island, 44°20.8′ N, 148°24.0′ E, 414 m, holotype (dv) ZISPb 57628, 24.7 mm length; **10.** *Scabrotrophon regina* (Houart, 1985), Philippine Islands, 13°14′ N, 120°31.6′ E, 682–770 m, holotype (dv) MNHN, 31 mm length.

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New and little known species of Pseudolividae (Gastropoda) from the Tertiary of Chile

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ABSTRACT

Two new species of Pseudolividae, *Macron vermeiji* and *Triumphis maitenlahuensis*, are described and figured from Miocene deposits of the Navidad Formation, central Chile. Both are among the oldest known representatives of their respective genera. Juvenile specimens of the Miocene species *Testallium cepa* (Sowerby, 1846) and the holotype of the Eocene *Sulcobuccinum retusum* (Philippi, 1887) are figured for comparison. One of the three syntypes of *Monoceros opimum* Hupé, 1854, and the holotype of *Monoceros labiale* Hupé, 1854 both previously considered synonyms of *Testallium cepa*, are figured for the first time and synonymy is confirmed.

INTRODUCTION

The earliest descriptions of Tertiary gastropods of Chile were by d'Orbigny (1842), Sowerby (1846), Hupé (1854), and Philippi (1887). Subsequently, a major revision of Pliocene/Pleistocene faunas was conducted by Herm (1969). New collections of Miocene gastropods from Chile made by the senior author and Klaus Bandel (Hamburg, Germany) and collections housed in the Museo Nacional de Historia Natural (Santiago, Chile) made by the junior author and the late Vladimir Covacevich (Santiago, Chile), include a number of undescribed species, among them the two new pseudolivid species described herein. The family Pseudolividae was recently revised by Vermeij (1998) who presented a reevaluation of the entire family based on shell characters of Recent and fossil species and his classification is followed herein. Vermeij (1998) attributed the family-name Pseudolividae in his abstract to Cossmann (1901) and in the systematic section to Fischer (1884). However, it was de Gregorio (1880, p. 101) who first introduced this name and the family is consequently attributed to him.

Although there is a continuous pseudolivid record in South America since the Late Cretaceous, few species have been described (Vermeij, 1997, 1998). Only three Chilean Tertiary species are known (Vermeij and DeVries, 1997): the Eocene *Sulcobuccinum retusum* (Philippi, 1887), the Miocene *Testallium cepa* (Sowerby, 1846), which also occurs in Peru, and the Pliocene *Testallium escalonia* Vermeij and DeVries, 1997.

Sulcobuccinum retusum comes from strata near the village of Algarrobo (Figure 1), north of San Antonio, Chile. From an intertidal platform of that village, Eocene and Late Cretaceous sediments are known. Because no material other than the holotype is known, and the genus *Sulcobuccinum* d'Orbigny, 1850, is known from the Campanian onward (Vermeij, 1998), the age of the species remains unclear. However, Vermeij (1998) regarded this species as of early Eocene age. *Gastridium retusum* Philippi, 1887, was reassigned to *Buccinorbis* Conrad, 1865, by Vermeij and DeVries (1997), a genus later considered to be a synonym of *Sulcobuccinum* (Vermeij, 1998). However, the holotype of *G. retusum* (Figures 13–14, SGO.PI 765, height 43 mm) has never been figured since the original drawing was published by Philippi (1887). The remaining species reported here come from the Navidad Formation (Figure 1).

ABBREVIATIONS

MNHN-LG: Muséum national d'Histoire naturelle, Laboratoire de Géologie, Paris, France. SGO.PI: Museo Nacional de Historia Natural, Departamento de Paleontología de Invertebrados, Santiago, Chile. SMF: Senckenberg Museum, Frankfurt, Germany.

SYSTEMATIC PALEONTOLOGY

Family Pseudolividae de Gregorio, 1880
Genus *Macron* H. and A. Adams, 1853

Type Species: *Pseudoliva kellettii* A. Adams, 1855 (= *Buccinum aethiops* Reeve, 1847) Recent, West Mexico.

Macron vermeiji new species
(Figures 7, 8, 10, 11)

Description: Shell medium-sized, ovate, spire low, consisting of five to six whorls. Height-to-width ratio

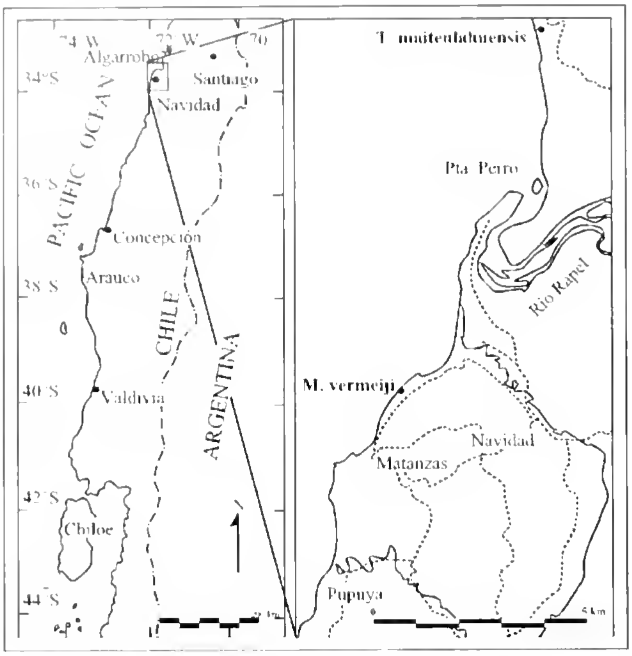


Figure 1. Type localities of *Macron vermeiji* and *Triumphis maitenlahuensis* and other localities mentioned in the text.

1.25. Whorls separated by narrow suture. Last whorl large, comprising 83% of total shell height, rounded, constricted basally above siphonal fasciole. Pseudolivid groove situated low on last whorl, terminating in distinct labral tooth. Spiral sculpture consisting of three cords below pseudolivid groove and very faint threads above, axial sculpture absent except for faint growth lines. Protoconch unknown. Outer lip planar. Anterior notch present, reflected as groove inside last quarter of last whorl. Interior of outer lip lirate. Columellar callus cutting deeply into former whorl, having two weak folds at entrance to siphonal canal. Columella with two weak folds at entrance to siphonal canal. Siphonal fasciole prominent, bounded above by keel. Anterior notch deep, no umbilicus.

Type Material: Holotype SGO.PI.5988 (height 24 mm, width 19 mm), paratype SGO.PI.3711 (height 22.5 mm; together with nine juvenile specimens of *Testallium cepa*). Early late Miocene (Tortonian), Navidad Formation.

Type Locality (Figure 1): About one kilometer north of Matanzas, Chile. Early late Miocene (Tortonian), Navidad Formation (see Frassinetti and Covacevich (1993) for more details on the locality).

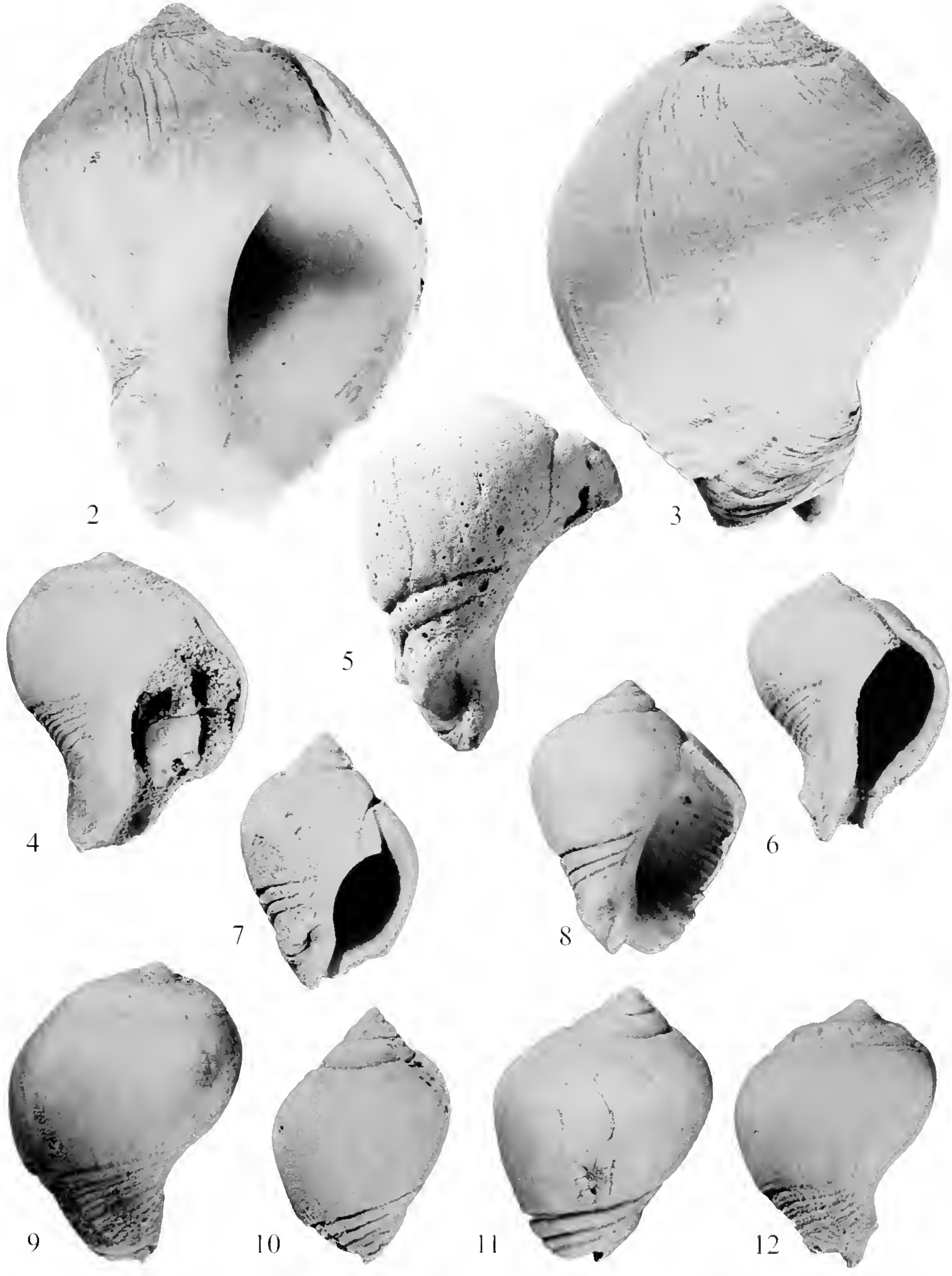
Occurrence: Specimens of the new species of *Macron* were collected on an intertidal platform about 1 km north of the village of Matanzas as described by Frassinetti and Covacevich (1993) and from a fossil bearing lens about 2 m higher in the section. That lens, however, was severely eroded the following year. It has been dated as Tortonian (upper Miocene) based on Foraminifera (Finger et al., 2003). The accompanying gastropod fauna indicates mainly a shallow-water environment but some possible deep-water species are present (Nielsen and DeVries, 2002), such as *Xenophora paulinae* Nielsen and DeVries, 2002. A deep-water environment is also indicated by benthic Foraminifera, the ostracod assemblage (Finger et al., 2003), and the presence of otoliths of fish species in the genus *Steindachneria* (Nolf, 2002). This contrasting evidence may be due to slumping of shallow-water sediments into deeper water, a model supported by the presence of reworked mudstone clasts. The sedimentology of these deposits was discussed elsewhere (Encinas et al., 2003).

Etymology: Named in honor of G. J. Vermeij (University of California, Davis, Geology) who contributed greatly to the knowledge of the Pseudolividae.

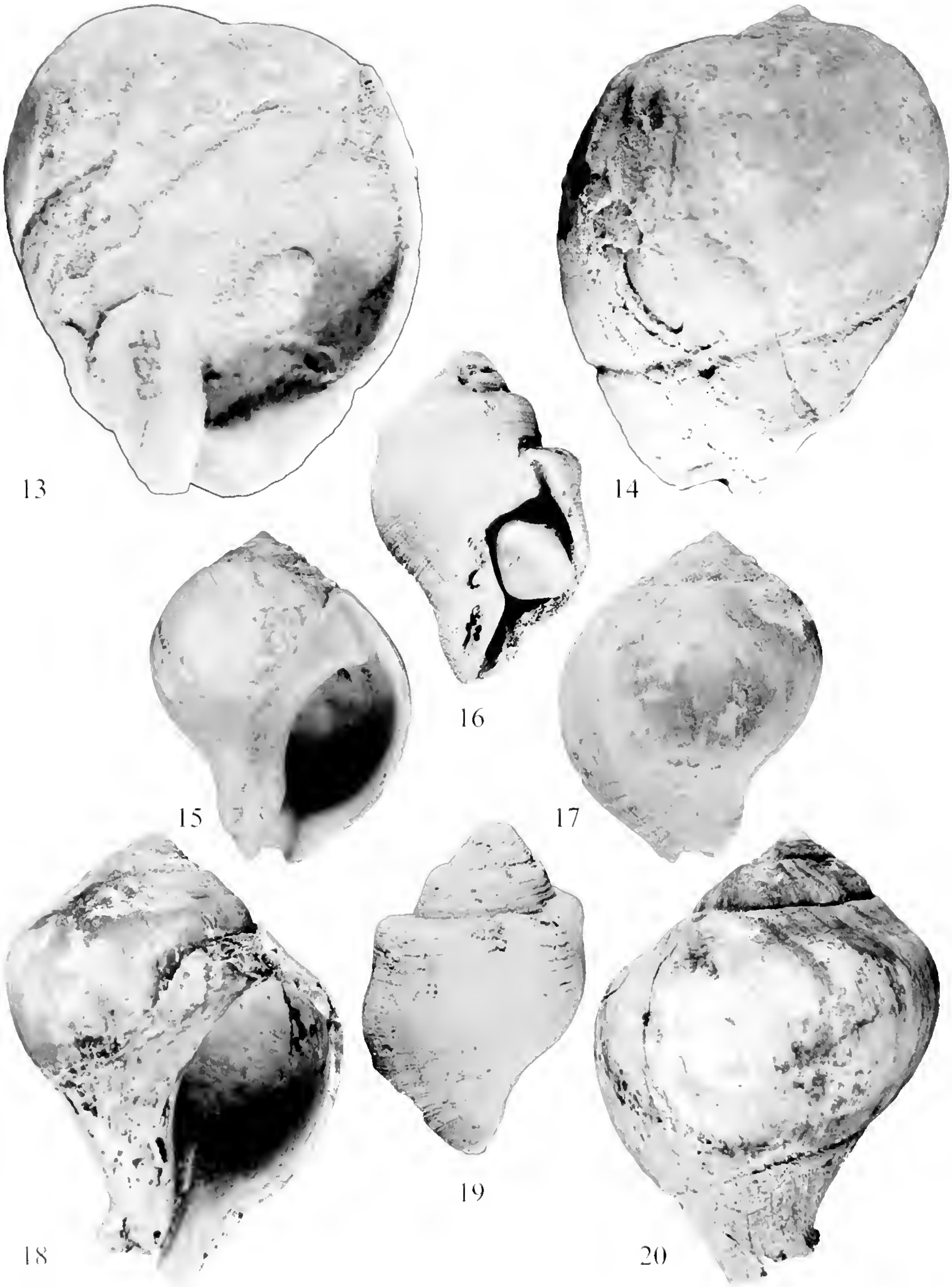
Discussion: Another possibly conspecific specimen is SGO.PI.766 (Figure 5, height 30.9 mm) from Navidad. Other species from the Tertiary of Chile resembling *Macron vermeij* are the Eocene *Sulcobuccinum retusum*, and the Pliocene *Testallium escalonia*. *Sulcobuccinum retusum* has the pseudolivid groove situated high on the last whorl and is smooth inside the outer lip. Juvenile specimens of *Testallium cepa* (Figures 4, 6, 9, 12, both part of SGO.PI.3711) of about the same size as presumably adult *Macron vermeiji* differ in not having lirae inside the outer lip, in having more numerous spiral elements below the pseudolivid groove, and in having the columellar callus secreted onto former whorls, rather than cutting deeply into them. Most of the larger specimens of *Testallium cepa* (Figures 2, 3, part of SGO.PI.3711, height 16 mm) have additional spiral elements above the pseudolivid groove and a more globose appearance, characters that are even more prominent in adults. The Pliocene *Testallium escalonia* has a higher spire, stronger spiral sculpture and no lirae inside the outer lip.

The spire of *Macron vermeiji* is relatively much lower than that of any previously known species of *Macron* (height-to-width ratio 1.25 in *M. vermeiji* compared with 1.9 to 4.1 in other species) and its last whorl is relatively larger (83% of total shell height compared with 68 to 74% in other species) so that the diagnosis of the genus given by Vermeij (1998) must be emended to include this species.

Macron vermeiji extends the geographic distribution of the otherwise strictly northern Pacific genus *Macron* into the southeastern Pacific. It is the lowest-spired species of *Macron* and thus closely resembles species of *Pseudoliva* Swainson, 1840, from which it mainly differs by the lirate interior of its outer lip. It is not only intermediate in shell-form but also comes from an area geographically between the mainly northeast Pacific *Macron* and the South African *Pseudoliva*. These genera have their origins in the (lower) Miocene of Venezuela (*Macron*; Gibson-Smith et al., 1997) and Madeira (*Pseudoliva*; Vermeij, 1998).



Figures 2–12. Pseudolividae from the Navidad Formation. **2–4, 6, 9, 12.** *Testallium cepa* (Sowerby, 1846). **2, 3.** Adult specimen SGO.PI.3714, height 46 mm. **4, 9.** Juvenile specimen SGO.PI.3714, height 26.3 mm. **6, 12.** Juvenile specimen SGO.PI.3714, height 23.5 mm. **5, 7, 8, 10, 11.** *Macron vermeiji* new species. **5.** cf. *Macron* cf. *vermeiji*, plaster cast of SGO.PI.766, height 30.9 mm (photo courtesy of T. J. DeVries). **7, 10.** Paratype SGO.PI.3714, height 22.5 mm. **8, 11.** Holotype SGO.PI.5988, height 24 mm).



Figures 13–20. Pseudolividae from the Chilean Tertiary. **13, 14.** *Sulcobuccinum retusum* (Philippi, 1887). Holotype SGO.PI.765, height 43 mm. **16, 19.** *Triumphis maitenlahuensis* sp. nov. Holotype SGO.PI.5523, height 29 mm. **15, 17, 18, 20.** *Testallium cepa* (Sowerby, 1846). **15, 17.** Syntype of *Monoceros opimum* Hupé, 1854, MNHN LG Gg2002.70, height 58 mm. **18, 20.** Holotype of *Monoceros labiale* Hupé, 1854, MNHN LG Gg2002.71, height 80 mm.

Genus *Testallium* Vermeij and DeVries, 1997

Type Species: *Gastridium cepa* Sowerby, 1846, Miocene, Chile.

Testallium cepa (Sowerby, 1846)
(Figures 2–4, 6, 9, 12, 15, 17, 18, 20)

Discussion: *Testallium cepa* has been discussed in detail by Vermeij and DeVries (1997) and it is present at most Miocene localities from southern Peru (DeVries and Frassinetti, 2003) to Isla Stokes, southern Chile (Frassinetti, 2001) and abundant in the Navidad Formation. However, juvenile specimens (Figures 4, 6, 9, 12) have not been figured and the three syntypes of *Monoceros opimum* Hupé, 1854 (Figures 15, 17; MNHN-LG Gg2002/70; height 58 mm) and the holotype of *Monoceros labiale* Hupé, 1854 (Figures 18, 20, MNHN-LG Gg2002/71; height 80 mm), put into synonymy with *Testallium cepa* by Vermeij and DeVries (1997), were unavailable at that time because the location of the collection described by Hupé was unknown. Rediscovery of Hupé's types in the MNHN-LG allows us to figure those specimens herein, confirming the inferred synonymy. According to new data its stratigraphic range is lowermost (DeVries and Frassinetti, 2003) to upper Miocene (Finger et al., 2003).

Genus *Triumphis* Gray, 1857

Type Species: *Buccinum distortum* Wood, 1828; Recent, Caribbean Sea.

Triumphis maitenlahuensis new species
(Figures 16, 19)

Description: Shell moderately large with stepped whorl profile. Protoconch unknown. Whorls with steep, almost straight, slightly concave sides. Last whorl with strong, ridge-like shoulder. Whorl slightly constricted below shoulder, forming a concave area followed by convex, globose region. Whorl anteriorly constricted and thus well defining short, slightly twisted siphonal canal. Broad, flat primary spiral cords present on whole whorl, two to three finer secondary cords between them. Axial sculpture of low, blunt nodes between suture and periphery present on early whorls, becoming obsolete on last whorl. Aperture oval, columella smooth with weak fold at opening of siphonal canal. Outer lip unknown. Siphonal fasciole strongly developed. Pseudoumbilicus formed by fasciole and inner lip might be an artifact caused by erosion. Height 29 mm.

Type Material: Holotype SGO.PI.5523.

Type Locality (Figure 1): Early late Miocene (Tortonian), Navidad Formation. At the coastal cliff about 500 m south of the Estero Maitenlahue, Chile to the north of Río Rapel, at locality 1409764 of Covacevich and Frassinetti (1986).

Occurrence: The new species of *Triumphis* was collected about 500 m south of Estero Maitenlahue to the north of Río Rapel (at the upper margin of Figure 1). This specific locality has not been dated, but nearby localities indicate a Tortonian (upper Miocene) age (Finger et al., 2003).

Etymology: Named after the type locality near the Estero Maitenlahue, Chile.

Discussion: *Triumphis* has been included in the family Buccinidae Rafinesque, 1815 by most workers (e.g. Keen, 1971), but Vermeij (1998) transferred it to Pseudolividae and this is followed here. Apart from the Recent type species, *Triumphis distorta*, only one poorly preserved specimen of *Triumphis* sp. from the middle Miocene of Kern County, California has been reported (Addicott, 1970). *Triumphis maitenlahuensis* differs from *Triumphis distorta* in being constricted below the ridge-like shoulder, in having subequal spiral ornament, and in having a well-defined siphonal canal. It differs from species of the similar genus *Nicema* Woodring, 1964, by having its ridge-like shoulder as an exterior projection of the posterior notch at the suture and not below the notch and suture. *Nicema* was considered to belong to the buccinid subfamily Photinae Troschel, 1867, by Vermeij (1998). *Triumphis maitenlahuensis* could be an intermediate species between *T. distorta* and the genus *Nicema*; however, as Vermeij (1998) adequately observed, "anatomical data and molecular sequences will be needed to confirm the phylogenetic affinities of *Triumphis*" (p. 73), and "anatomical observations on the living *N. subrostrata* will be needed to confirm assignment of *Nicema* to the Photinae" (p. 74).

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Notice

70th Annual Meeting
American Malacological Society
Sanibel Island, Florida
31 July–4 August 2004

I am glad to announce that the 70th Annual Meeting of the American Malacological Society will take place on beautiful Sanibel Island, Florida, from Saturday, July 31 to Wednesday, August 4, 2004. Sanibel Island is a world-renowned, nature-oriented travel destination that is also famous for its bountiful molluscan resources. The event will be hosted by The Bailey-Matthews Shell Museum and will have as its main venue the Sundial Beach Resort, located on the eastern part of the island.

Sanibel Island, Florida

The American Malacological Society is a dynamic international society of individuals and organizations with an active interest in the study and conservation of mollusks. AMS covers a wide range of subjects in the field of molluscan studies, and its meetings, symposia, sessions, posters, and special events reflect that.

A symposium on the Relationships of the Neogastropoda will be convened by M. G. Harasewych of the National Museum of Natural History at the Smithsonian Institution. Special sessions will include Biodiversity of Marine Mollusks (organized by Gustav Paulay, Florida Museum of Natural History); Coastal Molluscan Assemblages as Environmental Indicators (Michael Savarese, Aswani Volety, and Greg Tolley, Florida Gulf Coast University); Systematics of Freshwater Gastropods (Russel Minton, Louisiana State University); Global Marine Bivalve Database Workshop (Gustav Paulay, Florida Museum of Natural History, Paul V. Scott, Santa Barbara Museum of Natural History, and Graham Oliver, National Museums and Galleries of Wales), and Terrestrial Mollusks as Agricultural and Environmental Pests (David Robinson, United States Department of Agriculture/Academy of Natural Sciences of Philadelphia). In addition, a special forum organized by Ken Hayes, Anna Bass, and Amy Wethington, all graduate students in malacology, will focus on and discuss common issues and problems faced by soon-to-be professionals in the field.

The 70th Annual Meeting will be sponsored by the American Malacological Society, The Bailey-Matthews Shell Museum, and the Sanibel-Captiva Shell Club, with additional support from the Sanibel-Captiva Chamber of Commerce, Sundial Beach Resort, J. N. "Ding" Darling

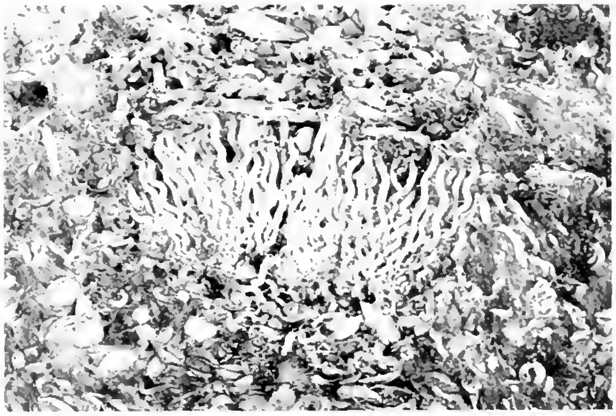
National Wildlife Refuge, Florida Gulf Coast University, and Captiva Cruises.

The Sanibel-Captiva Shell Club will sponsor the Shell Museum Open House on Sunday, August 1. The closing banquet will be a dinner-cruise aboard Captiva Cruises's Lady Chadwick, a two-deck vessel holding 250 passengers.

Nautilus slide at Sundial Resort

Specially priced rates at the Sundial Beach Resort will be available for meeting participants at $110/night for regular rooms, $125 for the Gulf View rooms, and $175 for two-bedroom suites. Sundial is willing to accommodate up to 6 students per suite, which will help decrease the cost of accommodations for participants on a low budget.

Three field trips are planned for the last day of the meeting, Wednesday, August 4: A nature-watching visit to J. N. "Ding" Darling National Wildlife Refuge on Sanibel, guided by professional ornithologist and Shell Museum volunteer Dr. Jon Greenlaw; a daylong boat trip to Cayo Costa State Park guided by senior Shell Museum staff (located on isolated and undeveloped Cayo Costa, the park offers pristine views of the Gulf, dunes, lagoons, and opportunities for shell collecting; no live-mollusk collecting is allowed in the park or elsewhere in Lee County); and a visit to a Plio-Pleistocene fossil pit in Sarasota County guided by Roger Portell, invertebrate paleontologist at the Florida Museum of Natural History.



Pliocene fossil assemblage in Sarasota County

More than 24 airlines service Southwest Florida International Airport in neighboring Fort Myers (30 minutes from Sanibel). The Lee Island Coast region offers many opportunities for side trips on your own, depending on your interest: Edison-Ford Winter Estates, Miracles baseball games, and Everglades National Park, to name a few.

More information check the meeting Web site: www.shellmuseum.org/AMS/index.htm

Cordially,

José H. Leal, PhD
President, American Malacological Society

INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions) with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Science Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe/). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

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Kaicher's *Card Catalogue of World-Wide Shells*: A collation, with discussion of species named therein

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ABSTRACT

Kaicher's *Card Catalogue of World-Wide Shells* is a series of cards illustrating gastropod mollusks, with one species being shown on each card. More than 6300 cards illustrating about 5860 species were issued in 60 "packs" between 1973 and 1992. These cards are especially important as many show type specimens. All packs and the range of the cards included in each are collated, as are changes and corrections to the cards made by Kaicher, other authors, and herein. The status of missing card numbers is clarified: some were accidentally skipped, others were removed by Kaicher before publication.

Nine species were inadvertently named in the *Card Catalogue*; all have short descriptions and therefore are not nude names. Type material for eight of these is detailed, with designation of six lectotypes. *Calliostoma vincentae* Kaicher, 1986, probably is a synonym of *Calliumbonella suturalis* (Philippi, 1836) (Trochidae); *Natica variolaria* Kaicher, 1981, becomes *Notocochlis variolaria* (Naticidae), **new combination;** *Amaea teramachii* Kaicher, 1980, is *A.* (*Scalina*) *sericogazea* (Masahito, Kuroda and Habe, 1971) (Epitoniidae), **new synonym**; *Haustrum ventricosum* Kaicher, 1980, is *Dicathais orbita* (Gmelin, 1791) (Muricidae), **new synonym**; *Terebra delicatula* Kaicher, 1981, is *T. alba* (Gray, 1834) (Terebridae), **new synonym**; *Conus alexandrinus* Kaicher, 1977 (Conidae) is the valid name for *C. musivus* Trovão, 1975, *non C. musivum* Sowerby, 1833 and its replacement name, *C. teresi* Trovão, 1978, **new synonyms**; *Conus lineopunctatus* Kaicher, 1977, is the valid name for *C. guttatus* Kiener, 1845 *non Cucullus guttatus* Roding, 1798 (a *Conus*), and its replacement name, *Conus neoguttatus* da Motta, 1991, **new synonyms**; *Conus lobitensis* Kaicher, 1977, is *C. fuscolineatus* Sowerby, 1905, **new synonym**; and *Conus negroides* Kaicher, 1977, is the valid name for *C. gabrielae* Rolán and Röckel, 2000, **new synonym.** A first reviser's choice is made for the spelling of *Epitonium oyasiouensis* Ozaki, 1958, which is judged not to be a senior synonym of *Amaea sericogazea*.

INTRODUCTION

Sally Diana Kaicher (1922–1999) was a professional illustrator and writer who worked at various times at the Academy of Natural Sciences in Philadelphia (ANSP), the National Museum of Natural History at the Smithsonian Institution (USNM), and the United States Department of Agriculture. She authored or illustrated several popular works on natural history, including Kaicher (1956–1957), Reid (1967), Epple (1969) and Reid et al. (2001), which is a revision of Reid (1967). She authored two scientific papers: Kaicher (1972) and Lyons and Kaicher (1978). She also illustrated and in some cases authored about twenty 35 mm filmstrips for classroom instruction, including one on mollusks (Kaicher, 1968). Germon and Lyons (1999) published a biographical sketch giving details of her career as well as photographs. Petuch (1980) published biographical notes and Lamprell (1999) and Rice (1999) published obituaries.

In 1973 Kaicher began publishing the *Card Catalogue of World-Wide Shells*. The *Card Catalogue* is a series of 3″ × 5″ (7.6 × 12.7 cm) glossy cards, each card illustrating a single species of gastropod mollusk with one or more black and white photographs. They were issued in "packs" of 97 to 106 cards, most packs being restricted to species of a single family. In addition to the species cards, each pack had a cover card and one or two introductory and acknowledgment cards. Production of the packs was irregular but continued until 1992. A total of 60 packs and 6437 cards were issued, including 6316 cards illustrating specimens, 60 cover cards, 60 acknowledgment cards, and one card, in Pack 31, discussing ovoviviparity in *Nassarius*. All of the species illustrated are prosobranchs, and almost all are marine, exceptions being freshwater or brackish species of *Neritina* (Neritidae), *Clea* (Buccinidae), and *Rivomarginella* (Marginellidae). Callomon (1999a) published on the Internet a list of the species illustrated in each part of the *Card Catalogue* and an index to the specific names (1999b).

About 5860 distinct species are illustrated, the total being less than the number of cards because some subspecies and varieties were illustrated, and because Kaicher reissued cards for some species or corrected their identifications. Kaicher issued replacement cards at different times for a variety of reasons. A small slip enclosed with Pack 16 announced that "some of these cards are unacceptably dark" and that those cards "will be reprinted and sent to you . . . without charge." At least 16 cards in Pack 16 were later replaced and mailed with Pack 17 (10 cards) and Pack 18 (6 cards). The replacements were noted only by a small typed slip with Pack 17 stating "Muricidae replacements . . . more with next pack." If a card was replaced because of poor image quality, the replacement card bears the same number. If a card was replaced to update the taxonomy or illustrate a better specimen, the replacement card has the original and new numbers separated by a slash [/], sometimes with the addition of "A" to the original number.

Kaicher published the *Card Catalogue* as an aid to both shell collectors and to professional malacologists. It is now routinely used as a tool by molluscan systematists and has been cited in numerous scholarly works. Many of the shells illustrated on the cards are type specimens never before illustrated photographically. Kaicher photographed many thousands of specimens, some in her own collection, others borrowed from private and institutional collections, and many during her travels to numerous major museums, both in America and abroad. Kaicher bequeathed her collection of Nassariidae to ANSP. Her family subsequently donated to ANSP the remainder of her shell collection, and her photographic negatives, notebooks, and correspondence.

As often happens when type material is illustrated or discussed, some lectotype designations were inadvertently made in the *Card Catalogue*. In part because of this, Kabat (1996) petitioned the International Commission on Zoological Nomenclature to suppress the *Card Catalogue* for nomenclatural purposes. Comments on the petition by various workers were published in *Bulletin of Zoological Nomenclature* 53: 273–277 and 54: 39–66, with the result that in Opinion 1905 (1998), the Commission ruled that the *Card Catalogue* is nomenclaturally available. We note that the fourth edition of the *International Code of Zoological Nomenclature* clarifies that lectotype designations made by inference of a holotype have standing only if "the original description neither implies nor requires that there were syntypes" (Article 74.6). Thus in some cases in which Kaicher had been thought to have inadvertently designated a lectotype, it will be found she did not in fact do so.

Because the *Card Catalogue* is available for nomenclatural purposes, it is important to have a collation, so that citations of nomenclatural actions therein can be made accurately. In cover notes that accompanied the packs, Kaicher corrected mistakes made in numbering the cards and others errors, mostly in spelling or identification. As recipients did not necessarily retain these notes, we have detailed them in our collation. Included are all changes suggested by Kaicher in cover notes and elsewhere. We have not attempted to review all nomina or to bring the names up to date although we have noted some necessary changes. The Marginellidae species treated by Kaicher in Packs 1, 26, and 60 have been extensively reviewed and brought up to date by Coovert (1999). Coovert notes that 159 of 308 marginellid cards illustrate type specimens. In the References Cited we give the full citation for each pack, taking into account missing and duplicated numbers.

RESULTS

VALIDATED NAMES

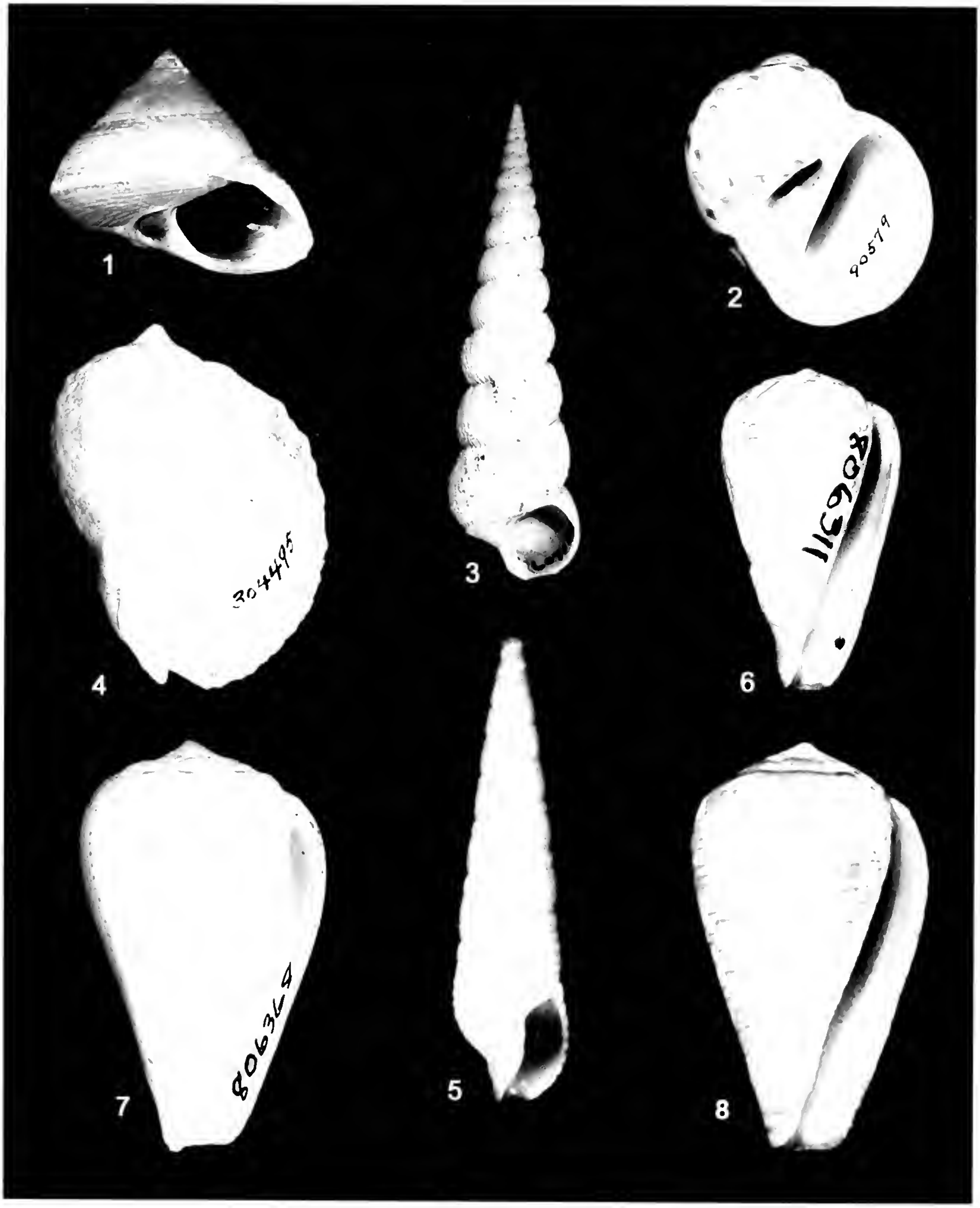
Nine manuscript names attributed to various authors appear to have been inadvertently validated in the *Card Catalogue*. In each case, Kaicher seems to have taken the name from a label in a collection, and in each case she provided a short description. The International Code of Zoological Nomenclature (ICZN, 1999) does not prescribe any minimum length for a description, so these are not nude names as has been maintained by some authors, e.g., Rolán and Röckel (2000), Rolán and Ryall (2000). Also, Kaicher used the *Card Catalogue* to illustrate species that she considered to be valid, thereby fulfilling the requirement of ICZN Article 11.5, that a name be used as valid when proposed. In the context of the *Card Catalogue*, Kaicher provided comparative illustrations of many congeneric or confamilial species for each of the validated names. Although Kaicher was unaware that she was the first to validly introduce these names into the literature, ICZN Article 16.1 does not require that names published before 2000 be explicitly indicated as new. We therefore attribute authorship of these names to Kaicher. We have located type material for eight of the nine names: six at the United States National Museum, Smithsonian Institution (USNM) on August 16, 2000, one in the type collection of The Natural History Museum, London (BMNH) and one at The Academy of Natural Sciences, Philadelphia (ANSP).

Calliostoma vincentae Kaicher, 1986 (Figure 1, 9–11). Attributed to "Ruttelant" on Card 1614. Shells of this species have been sold for many years as "*Calliostoma vicentae* Rutllant" being listed, for example, by Rice (1969–2000), but had not been formally published before Kaicher's treatment. Dr. Juan Rutllant y Bassets of Melilla, Spanish Morocco, was a member of the Malacological Society of London from 1947 until 1951 or 1952, his name appearing in the membership list published in the Society's *Proceedings* in 1951 (vol. 28, p. 258), but not in the one published in 1953 (vol. 29, pp. 259–265). He distributed specimens with the manuscript name *Calliostoma vicentae*, as noted by Mienis (2002), whose research shows that Rutllant did not publish on mollusks. Rice (2000) spelled the name "vicenta", and Santos Galindo (1977), where it is a nude name, attributed it to "Ruthland."

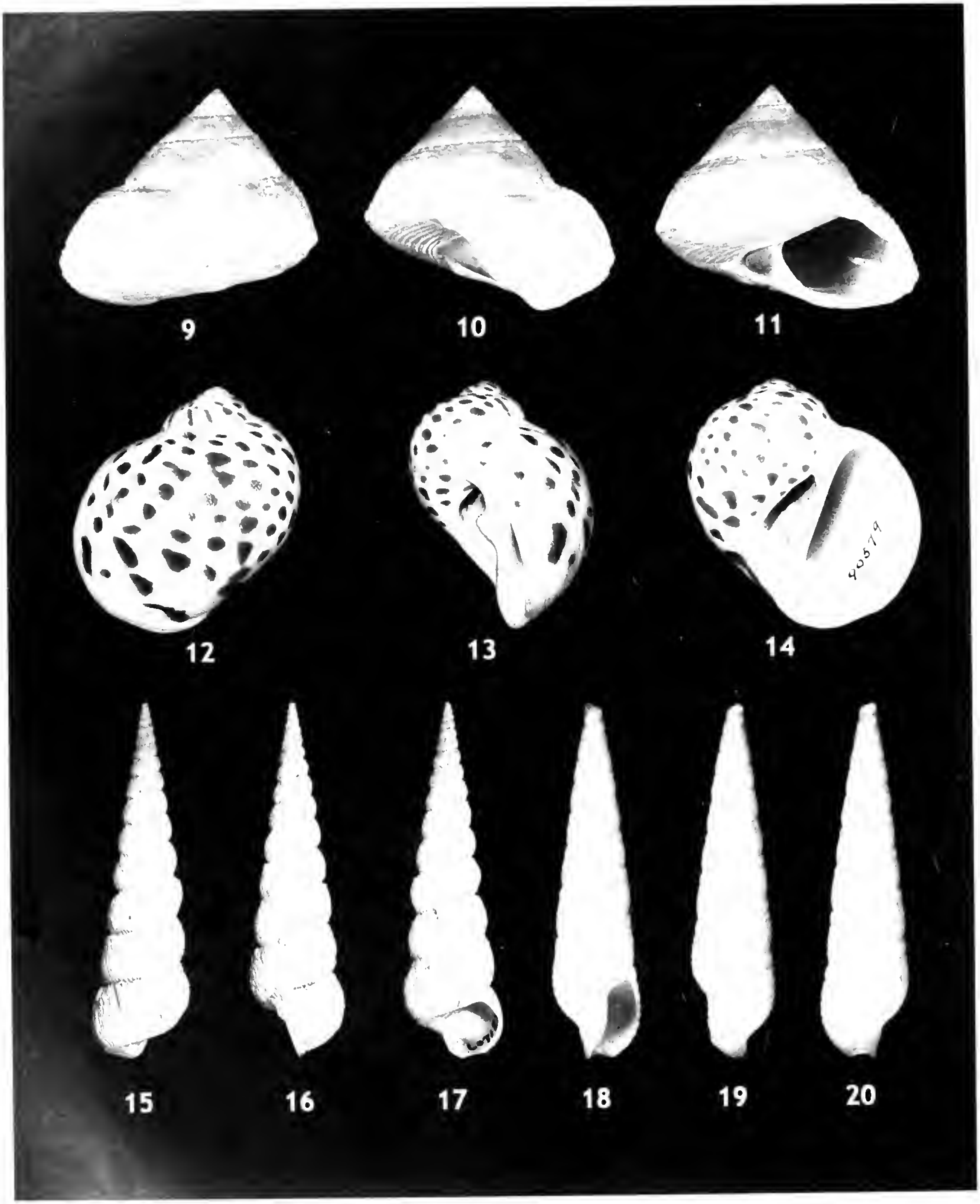
The type lot is ANSP 198989, which is labeled as "Calliostoma vincentae Rutllant, Melilla arrastre, J. F. C. Ojeda! 1956 Spanish Morocco". The original label gives the name as "Calliostoma vicentae Rutllant". The lot contains two specimens; to fix the identity of the name, we here designate the figured specimen as the lectotype (Figure 1, 9–11) (height 13.7 mm, the paralectotype is 13.0 mm in height). Two opercula and crumbled dried animals are also in the lot, but it is not possible to determine what is part of the lectotype and what part of the paralectotype.

Although the manuscript name was "vicentae" Kaicher validated it as "vincentae", a spelling that must stand. Poppe and Goto (1991) and Mienis (2002) synonymized it with *Callumbonella suturalis* (Philippi, 1836).

Natica variolaria Kaicher, 1981 (Figure 2, 12–14). Attributed to Recluz on Card 2961. Recluz introduced this name in



Figures 1–8. Primary type specimens of species named by Kaicher. **1.** *Calliostoma vincentae* Kaicher 1986 lectotype ANSP 198989 height 13.7 mm. **2.** *Natica variolaris* Kaicher 1981 lectotype USNM 90579 height 33.4 mm. **3.** *[illegible]* Kaicher 1980 lectotype USNM 607188 height 43.8 mm. **4.** *Haustrum [illegible]* Kaicher 1980 holotype USNM 304495 35.6 mm. **5.** *Terebra delicatula* Kaicher 1981 holotype BMNH 1911.8.22.273 8.9 mm. **6.** *Conus alexandrinus* Kaicher 1977 lectotype USNM 806311 height 23.6 mm. **7.** *Conus lineopunctatus* Kaicher 1977 lectotype USNM 806368 height 58.1 mm. **8.** *Conus [illegible]* Kaicher 1977 lectotype USNM 806331 height 19.0 mm.



Figures 9–20. [illegible] named by [illegible] **9–11.** [illegible] 1986, lectotype ANSP 198989 [illegible] **12–14.** [illegible] 1981, lectotype USNM [illegible] height [illegible] mm. **15–17.** [illegible] height [illegible] mm. **18–20.** [illegible] 1981, holotype BMNH 1911.8.22.27 [illegible]

the synonymy of *Natica fanel* Recluz, 1844 (ex Adanson 1757, non-binominal) in the original description of that species. Reeve (1855) and Tryon (1886) listed it as a synonym of *Natica pellistigrina*. Dixon and Ryall (1985, pp. 13–14) stated that ". . . [*Natica variolaria*] has been used correctly in its West African context by several authors within the last twenty years," but gave no references. Similarly, Verberekt (1995) said "About twenty-five years ago, the name *Natica variolaria* Récluz, 1844 was introduced as the valid name for this species." Correspondence with Verberekt (through A. Verhecken, in e-mail to REP, 30 January 2000), failed to reveal a reference of this vintage. The only such use we have found is by Santos Galindo (1977), where *Natica variolaria* is a nude name. Since the name was not used as valid before 1961, it cannot be attributed to Recluz, where it first appeared in synonymy (ICZN Article 11.6). Kaicher (1981) apparently was the first to use the name as valid and provide a description, and therefore must be attributed with the authorship.

The type lot, cited by Kaicher, is USNM 90579 and is labeled as "Natica pellis-tigrina Chem. W. Africa Wesleyan Univ." and which contains a single specimen. The name "*Natica variolaria*" does not appear on the label. Kaicher may have inferred the name from the position in the USNM collection, where the species is currently filed as *Notocochlis variolaria*, attributed to Recluz, 1844. Kaicher may have seen a second lot, adjacent in the collection: USNM 272979, with USNM label "Natica variolaria Rec. Gabon, Africa. Deyrolle" and original label with "Natica variolaria Recl. Gabon." handwritten and "Emile Deyrolle 46, rue de Bac. Paris . . ." typeset. We cannot prove that Kaicher saw this second lot because the naticid collection at USNM was reorganized by Alan Kabat subsequent to Kaicher's work. To fix the identity of the name, we here designate Kaicher's figured specimen, USNM 90579, as the lectotype (height 33.4 mm); USNM 272979 contains two possible paralectotypes (heights 18.6 and 15.6 mm). It is not clear to us that these two specimens are conspecific with the lectotype; their spires are lower and have stronger axial ribbing below the suture.

Natica variolaria was first published in synonymy of *Natica fanel* Recluz, 1844 (ex Adanson, 1757, non-binominal), which is preoccupied by *Cochlis fanel* Röding, 1798 if the latter is classified as a *Natica*. Fernandes and Rolán (1993) synonymized Röding's taxon with *Natica hebraea* Martyn, 1784, a non-binominal name conserved in ICZN Opinion 1662 in 1992. *Natica fanel* Recluz, 1844 is a synonym of the West African *Natica rocquignyi* Fischer-Piette, 1942 according to Fernandes and Rolán (1993), but an earlier name, based on Adanson's taxon, is *Natica multipunctata* de Blainville, 1825, as noted by Verberekt (1995) and Kabat, Finet and Way (1997). *Natica variolaria* Kaicher, however, is not conspecific with *Natica multipunctata*, having a sparser pattern and a broader cord in the umbilicus. Alan Kabat (pers. comm. to GR, 21 July 2001) confirms that he considers this species to be a *Notocochlis* as reflected in the arrangement of the USNM collection.

Amaea teramachii Kaicher, 1980 (Figure 3, 15–17). Attributed to Kuroda on Card, 2358, but he did not publish the name; it is not listed by Hanshin Shell Club (1986) or Higo et al. (1999). The name has appeared in print several times as a nude name attributed to Kuroda MS (e.g., Azuma 1960, Higo 1973). Weil et al. (1999) treat the species as valid, attributing the name to Kuroda and Habe, 1955, but do not provide a bibliographic reference. It is not listed among Habe's taxa by Okamoto (2001). Specimens have been distributed under this manuscript name for at least 50 years: ANSP 189370, identified as *A. teramachii* on the original label was purchased from Shigeo Hashimoto and catalogued in October 1952. The name must be attributed to Kaicher, the first author to provide a description and illustration.

The type lot, cited by Kaicher, is USNM 607188, with USNM label "Amaea splendida de Boury. Tosa, Shikoku, Japan. 100 fms ex J. H. Webb 1033 Acc. 200168" and original label "Amaea splendida Boury Tosa 100 fms. Japan"; it contains a single specimen. The name "*Amaea teramachii*" does not appear on the label; Kaicher may have inferred the name from the position in the USNM collection, where the species is currently filed under that name, attributed to Kuroda 1952. Kaicher likely saw a second lot, also with a single specimen, adjacent in the collection: USNM 605776, with USNM label "Amaea teramachii Kuroda. Tosa, Japan 150 fms. 1348" and original label "Amaea teramachi Kur Tosa 150 fms vaey [*sic*] rare". To fix the identity of the name, we here designate Kaicher's figured specimen, USNM 607188, as lectotype (height 43.8 mm); USNM 605776 is a paralectotype (height 33.6 mm).

Kaicher compared *Amaea teramachii* to *Amaea cerea* Masahito, Kuroda and Habe, 1971, but that species is currently placed in *Clathroscala* whereas *A. teramachii* belongs in the subgenus *Scalina* Conrad, 1865, of which four species are currently recognized from Japan (Higo et al., 1999). It differs from *A.* (*S.*) *gazeoides* Kuroda and Habe in Habe, 1961, in having a less elongate body whorl; from *A.* (*S.*) *mathildona* (Masahito, Kuroda and Habe, 1971) in being large, less slender and having more spiral cords per whorl; and from *A.* (*S.*) *splendida* Boury, 1913) in having finer sculpture. It is most similar to *A.* (*S.*) *sericogazea* (Masahito, Kuroda and Habe, 1971), from which Weil et al. (1999) distinguish it as having "more numerous spiral cords of varying strengths". Their illustrations of these species (figs. 242 and 362), however, do not support this difference, nor does examination of eight additional specimens identified as *A. teramachii* (ANSP 189370, 234720, 243251, 243242). We therefore consider *A. teramachii* to be a synonym of *A. sericogazea*.

Tsuchida (2000) synonymized *A. sericogazea* with *A. oyasioensis* Ozaki, 1958, which was named as a Pliocene fossil. Examination of Ozaki's illustration of the holotype shows that it has a channeled suture defined by a strong spiral cord with the other cords uniformly weaker. In *A. sericogazea*, the whorls are of uniform strength near the suture, but stronger below the periphery, particularly on the spire, which gives the early whorls an angular profile. *Amaea oyasioensis* also tapers more rapidly than does *A. sericogazea*; the width of the anterior whorl of the holotype is about 3.8 mm; the comparable measurement in *A. sericogazea* of the same height (18.5 mm) and number of whorls (4) would be about 6.7 mm. We therefore reject the synonymy of *A. sericogazea* with *A. oyasioensis*.

The heading of the original description is *Epitonium* (*Boreoscala*) *oyasioensis* (Ozaki, 1958, p. 142), but the spelling "*oyasioensis*" is used earlier on p. 142, in the plate caption (pl.15, fig. 23) and in the index (p. 180). The name refers to the Oyasio (or Oyashio) Current. Either specific name is acceptable nomenclaturally. If Oyasio is latinized, then an "n" is added, following the pattern of Latin words ending in "-io" (e.g., *dictio, dictionis*), which yields "*oyasionensis*"; if the word is not latinized, "-*ensis*" is added directly to the Japanese word, resulting in "*oyasioensis*". We select *oyasionensis* as the correct original spelling, judging it likely to be the better known because of its use by Tsuchida (2000).

Haustrum ventricosum Kaicher, 1980 (Figure 4, 21–25). Attributed to Tate on Card 2470, but not described by him; the name does not appear in any of his papers on Australian marine or fossil mollusks in the bibliography by Blake (1902).

The type lot, cited by Kaicher, is USNM 304495; the USNM label says "Purpura ventricosa Tate. G. of Spenser, South Australia. Bednall"; the original label says "Purpura ventricosa. Tate G. of Spencer Aus". The lot contains a single specimen, height 33.6 mm, which is the holotype.

The operculum is part of the lot (Figure 24–25).

The specimen is *Dicathais orbita* (Gmelin, 1791), a common and highly variable species in southern Australia. This identification was suggested by Dr. Winston F. Ponder, who examined the holotype on 16 August 2000.

Terebra delicatula Kaicher, 1981 (Figure 5, 18–20). Attributed to Preston on Card 2752, but Preston did not publish such a name; it is not listed by Adam (1971) or Bratcher and Cernohorsky (1987).

The holotype is in the type collection at BMNH, catalogue number 1911.8.22.273 (cited by Kaicher); the type locality is Martinique.

We consider this name to be a junior subjective synonym of *Terebra alba* Gray, 1834. Gray's name was recognized as valid by Bratcher and Cernohorsky (1987); Kaicher appears to be the first modern author to have recognized the taxon as a good species, although she did not discover the oldest name for it.

Conus alexandrinus Kaicher, 1977 (Figure 6, 30–32). Attributed to "Pais-da Franca" [*sic*] on Card 1293. Coomans, Moolenbeek and Wils (1980) stated that name was found on dealers' lists but was not published by Paes-da Franca. They, Rolán and Röckel (2000) and Filmer (2001) considered it a nude name introduced by Kaicher, but Kaicher does provide a brief description.

Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 806311. The USNM label says "Conus tevesi Trovao, 1978. Caota Bay, Angola 1976. In sand under rocks, 1–2 m. Acc. 340672." The original, handwritten by Ed Petuch, says "Conus tevesi Trovao, 1978 (= musivus Trovao, 1975, non Sowerby). In sand under rocks, 1–2 m depth. Coato Bay, Benguela, Angola—1976." To fix the identity of the name, we here designated the figured specimen, height 23.6 mm, as the lectotype (Figure 5, 30–31). A second specimen in the lot, height 24.1 mm is a paralectotype (Figure 32).

In the cover sheet to Card Pack 14, Kaicher synonymized the species with *Conus musivus* Trovão, 1975. Trovão (1978) replaced this name with *C. tevesi*, considering it a homonym of *C. musivum* Sowerby, 1833. However, "musivum" is a noun meaning mosaic; it would be a homonym of the adjective "musivus" only in a neuter genus, according to the examples provided in ICZN Article 58, concerning single letter differences between specific epithets. One of us (GR) posted this matter on the ICZN listserver (http://lyris.bishopmuseum.org/cgi-bin/lyris.pl?enter=iczn-list) on 29 August 2002. Replies indicated that commissioners favor amending Article 58 (under Article 78.3.3), which is on the agenda for the next meeting of the International Commission on Zoological Nomenclature. Therefore we consider *Conus musivus* Trovão to be preoccupied by *C. musivum* Sowerby, 1833, *C. alexandrinus* Kaicher, 1977 to be the valid name for the species, and *C. tevesi* Trovão, 1978 to be a junior objective synonym.

Edward J. Petuch (pers. comm. to GR, 26 January 2000) confirms that the specimens of this and the three following species were in his personal collection when Kaicher photographed them. Later he donated his collection of Conidae to USNM.

Conus lineopunctatus Kaicher, 1977 (Figure 7, 26–29). Attributed to Trovão on Card 1259, but not published by him, it is not listed by Kohn et al. (1995). Apparently this is a dealer's name; it is listed by Rice (1977).

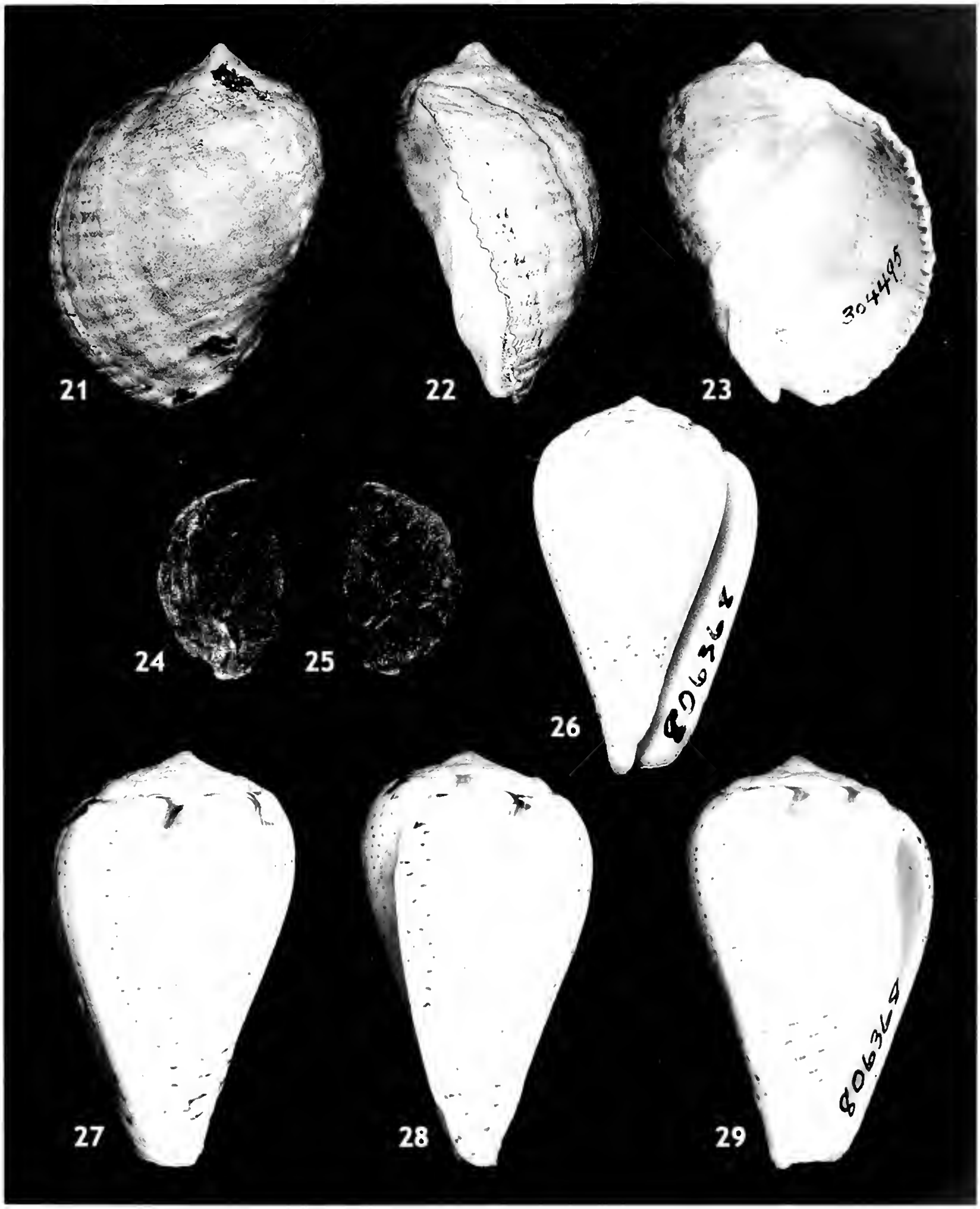
Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 806368. The USNM label says: "Conus lineopunctatus Trovao, 1976, off Baia dos Elefantes, Angola 1968, 20 m. Acc. 340672"; the original label, handwritten by Ed Petuch says: "Conus lineopunctatus Trovao, 1976 (= guttatus Kiener, 1849 non Roeding, 1798). Trawled 20 m depth off Baia dos Elefantes, Benguela, Angola—1968—sand bottom". To fix the identity of the name, we here designate the figured specimen, height 38.1 mm, as the lectotype (Figure 7, 27–29). A second specimen in the lot, height 34.7 mm, is a paralectotype (Figure 26).

This is a valid species; synonyms are *Conus guttatus* Kiener, 1845, *non Cucullus guttatus* Röding, 1798 (a *Conus*) and *Conus neoguttatus* da Motta, 1991, a replacement for Kiener's name. Rolán and Röckel (2000) and Filmer (2001) considered this a nude name but it had a brief description. The species that Röckel and Fernandes (1982) noted is "known to collectors as '*lineopunctatus*'" is a different taxon named *Conus micropunctatus* Röckel and Fernandes, 2000.

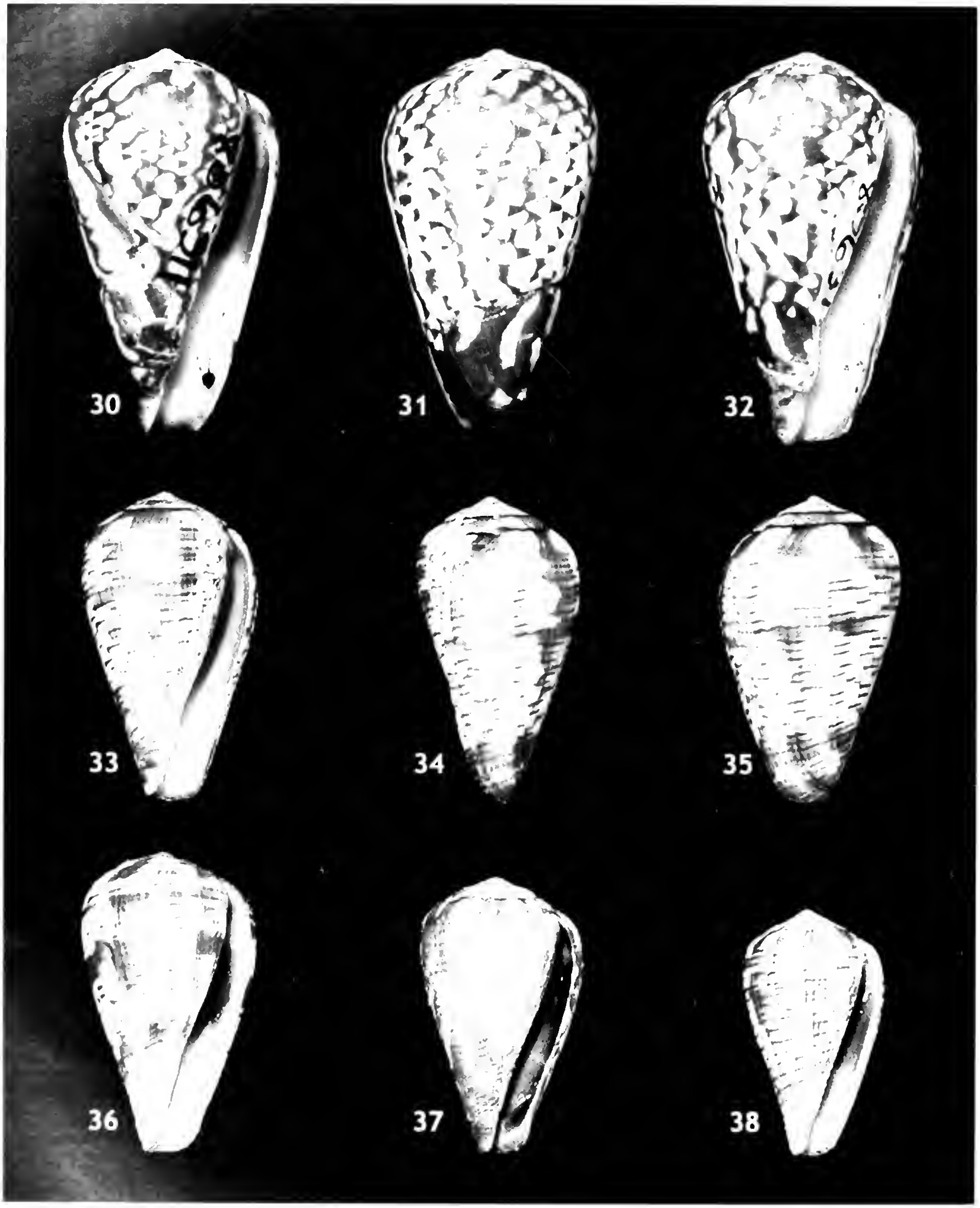
Conus lobitensis Kaicher, 1977 (Figure 8, 33–38). Attributed to Pais-da Franca [*sic*] on Card 1311, but she did not publish the name; it is not listed by Kohn et al. (1995). Apparently this is a dealer's name, but not offered recently according to Rice (1999).

Kaicher did not cite an institution or catalogue number, however, we found the figured specimen in USNM 806331. The USNM label says "Conus obtusus Kiener, 1849. Armado bay, Angola, 1975, under rocks, low tide. Acc. 340672"; the original label, handwritten by Ed Petuch says: "Conus obtusus Kiener, 1849 Under rocks, low tide, Armado Bay, Mocamedes, Angola—1975." To fix the identity of the name, we here designate the figured specimen, height 19.0 mm, as the lectotype (Figure 8, 33–35). The locality is thus Armado Bay, Angola, not Lobitos Bay, Angola as might be expected from the name. Three other specimens in the type lot, heights 18.7, 17.1, and 15.1 mm, are paralectotypes (Figure 36–38).

Rolán and Röckel (2000) and Filmer (2001) considered this a nude name, but it had a brief description. *Conus lobitensis*, however appears to be a synonym of *Conus fuscolineatus* Sowerby, 1905, as illustrated by Rolán and Röckel



Figures 21–29. Type specimens of species named by Kaicher. **21–23.** *Haustrum ventricosum* Kaicher, 1980, holotype, USNM 304495, 33.6 mm. **24–25.** Operculum of holotype of *Haustrum ventricosum*. **26.** *C. lineopunctatus*, paralectotype, USNM 806368, height 34.7 mm. **27–29.** *Conus lineopunctatus* Kaicher, 1977, lectotype, USNM 806368, height 38.1 mm.



Figures 30–38. [illegible] Kuchler. **30–31.** [illegible] Kuchler, 1977, lectotype USNM [illegible] **32.** [illegible] type USNM 806[illegible] **33–35.** [illegible] Kuchler, 1977 [illegible] USNM [illegible] **36–38.** [illegible] paralectotype USNM 806[illegible] height 18.7, 17.1, 15.4 mm.

Conus negroides Kaicher, 1977. Attributed to Pais-da Franca [*sic*] on Card 1313, but she did not publish the name; it is not listed by Kohn et al. (1995). Apparently a dealer's name, *Conus negroides* is attributed to Kaicher, 1977 by Rice (1999).

The location of the type material is unknown; we were unable to locate the figured specimen at USNM. The type locality is Angola, as listed by Kaicher.

Rolán and Röckel (2000) and Filmer (2001) considered this a nude name, but it had a brief description. Rolán and Röckel (2000) listed it in the synonymy of their new species *Conus gabrielae*, which is therefore a junior subjective synonym of *Conus negroides*.

For completeness, we note that Kaicher coauthored one species published outside the *Card Catalogue*, *Vexillum* (*Pusia*) *chickcharneorum* Lyons and Kaicher, 1978. *Leptoconus hawaiensis* "Bartsch and Rehder" is a nude name introduced by Kaicher (1956, part 5, pl. 5, fig. 6); it is a synonym of *Conus suturatus* Reeve, 1844 according to Kay (1979) and Filmer (2001). Rolán and Ryall (2000) listed *Conus lucirensis* as a nude name introduced by Kaicher, but that species was described by Paes-da Franca (1957).

List of Packs

Exact dates of publication for the card packs (Table 1) are difficult to determine. Most cover sheets (described below) are dated and we have used this date except where better evidence is available. Kaicher did not mail all packs of a given number at the same time, but posted them in small batches as she collated them. A few of Kaicher's records survive that have been helpful in dating. The cover sheet for Pack 42 is dated August 28, 1985 but it states that the cards would not be received from the printer until September 5. The earliest mailing record we have located for Pack 42 is September 9, and that date is used herein.

Cover Sheets and Errata Slips (Sheets)

Each pack was accompanied by a "cover sheet," indicated by CS herein. These small sheets were of varying sizes (11 to 14 cm wide and 11 to 28 cm long) and were not designed for permanency. The top of each usually had information about planned future packs and sometimes listed changes to be made on cards in previous packs. The bottom was an order form for the next card pack. In addition to the cover sheet, some packs included an "errata slip," listing changes to be made on cards already issued, indicated by ES herein. These slips were of various sizes, sometimes including only a single line of type, and were obviously not intended for retention after the changes had been made. For reference purposes we have assigned them numbers. All are assumed to have been issued with the like-numbered cover sheets unless otherwise stated but some might have been sent with subsequent packs. The following such slips have been identified:

ES5: stapled to CS5 (Mitridae).
ES23: undated (Epitoniidae).
ES29. slip pasted to CS29, with handwritten addition, possibly not to all copies.
ES37: undated (changes in Columbellidae).
ES40. undated, typewritten (magnification of *Coralliophila mansfieldi*).
ES42a: undated slip with CS42.
ES42b: undated slip with CS43 (wrapped around the replacement cards).
ES49a: dated 10 days after CS49 but sent with it.
ES49b: slip pasted to CS49.
ES58: probably issued with CS59.

Corrections and Annotations

We use the following conventions in the list of corrections and annotations:

1) Where species cards were not numbered, we assign them numbers that were skipped within the same pack, if Kaicher had not already done so.
2) In cases of reidentification, we add authors where Kaicher omitted them and inferred generic names in a few cases where Kaicher did not state them explicitly (e.g., 824); we have given years only if Kaicher gave them, which she sometimes did for recently named species.
3) For generic changes we state the combination if the ending of the trivial name or the use of parentheses changed, even if Kaicher omitted this information; otherwise we cite only the genus.
4) Underlining is changed to italics in quotations of Kaicher.
5) Each error that is corrected is attributed to a source, either a cover sheet [CS#], an errata sheet [ES#], another card [Card #], ourselves [herein] or another published work. For brevity, common errors are assigned the following numbers, to avoid repetitive explanations in the text.

Note 1: Number was inadvertently skipped (96, 145, 146, 369, 744, 1328, 1526, 1542, 2009, 2178, 2303, 3214, 3239, 3289, 3346, 5259, 5437, 5660, 5661, 5842, 6038, 6070, and 6193); in some cases reassigned to an unnumbered card. In addition, Kaicher removed cards 345, 2275, 2687, 2990, 3013 (in some cases), 5047 and 5757 before release.

Note 2: Number duplicated (745, 1540, 3137, 3288, 3770, 3776–3875, 5253, and 6189). Kaicher noted some of these duplications in her cover sheets, but did not recommend solutions. When the duplicates are in separate packs, the one published later can have "[bis]" (Latin for "twice") added to its number to distinguish it if desired. There was no order, alphabetic, taxonomic, or geographic, to the cards within a pack as issued, so for duplicate numbers within packs it cannot be determined which was intended to bear the number.

Note 3: Specific name is misspelled.

Table 1. Dates of publication of the *Card Catalogue*, with subject and range of card numbers included in each pack. Most dates were obtained from the cover sheets issued with the card packs; "KR" in brackets after a date indicates that it was obtained from Kaicher's records; "ES" means errata sheet.

Pack	Date of issue	Subject	Card numbers range
1	October, 1973	Marginellidae	1–98
2	December 19, 1973 [KR]	Muricidae I	99–195
3	February 15, 1974	Mitridae I	196–292
4	May 26, 1974	Mitridae II	293–389
5	September 5, 1974	Strombacea	390–497
6	December 14, 1974	Muricidae II	498–594
7	March 28, 1975	Terebridae I	595–691
8	August 15, 1975	Naticidae I	692–797
9	April 13, 1976 [KR]	Mitridae III	798–903
10	July 15, 1976	Volutidae	904–1009
11	November 15, 1976	Conidae I	1010–1115
12	January 10, 1977	Conidae II	1116–1221
13	March, 1977	Conidae III	1222–1327
14	June, 1977	Conidae IV	1329–1434
15	December 9, 1977 [KR]	Mitridae IV	1435–1540
16	March 2, 1978 [KR]	Muricidae III	1540–1646
17	June 1, 1978	Cymatiidae I	1647–1752
18	September 18, 1978 [KR]	Fasciolariidae I	1753–1858
19	December 6, 1978	Cancellariidae	1859–1964
20	April 18, 1979	Muricidae IV	1965–2071
21	November, 1979	Trochidae I	2072–2177
22	April 9, 1980	Trochidae II	2179–2284
23	July 2, 1980	Epitoniidae I	2285–2391
24	August 8, 1980	Thaididae I	2392–2497
25	December 15, 1980	Muricidae V	2498–2603
26	February 27, 1981	Marginellidae II	2604–2709
27	May 20, 1981	Terebridae II	2710–2815
28	July 17, 1981	Haliotidae	2816–2921
29	October 9, 1981	Naticidae II	2922–3027
30	December 23, 1981	Epitoniidae II	3028–3133
31	April 2, 1982	Nassariidae I	3134–3238
32	July 21, 1982	Cymatiidae II and Bursidae	3240–3345
33	November 20, 1982	Olividae I	3347–3452
34	March 27, 1983	Nassariidae II	3453–3558
35	July 27, 1983	Epitoniidae III	3559–3664
36	December 6, 1983	Cassidae and Oocorythidae	3665–3770
37	March 26, 1984	Columbellidae I	3700–3875
38	August 9, 1984	Columbellidae II	3876–3881
39	November 1, 1984	Turridae I	3882–3987
40	January 22, 1985	Coralliophilidae I	3988–4093
41	April 24, 1985	Nassariidae III	4094–4199
42	September 9, 1985 [KR]	Columbellidae III	4200–4305
43	November 6, 1985	Buccinidae I	4306–4411
44	February 20, 1986	Buccinidae II	4412–4517
45	May 23, 1986	Trochidae III	4518–4623
46	September 19, 1986	Fasciolariidae II	4624–4729
47	January 8, 1987	Neritidae I	4730–4835
48	May 10, 1987	Buccinidae III	4836–4941
49	August 15, 1987 [ES49a]	Olividae II	4942–5046
50	November 30, 1987	Trochidae IV	5048–5153
51	February 20, 1988 [KR]	Olividae III	5154–5258
52	August 10, 1988	Turbinidae I	5260–5365
53	December 15, 1988	Fissurellidae I	5366–5471
54	April 20, 1989 [KR]	Olividae IV	5472–5577
55	October 26, 1989	Turbinellidae I	5578–5685
56	March 27, 1990	Trochidae V	5686–5791
57	August 29, 1990	Buccinidae IV	5792–5897
58	March 12, 1991	Ovulidae I	5898–6003
59	August 17, 1991	Muricidae VI	6004–6109
60	May 14, 1992	Marginellidae III	6110–6215

Note 4: Specific name is a noun and hence invariant.
Note 5: Specific name is a genitive and hence invariant.
Note 6: Specific name is an adjective in comparative form and hence varies with gender of genus.
Note 7: Generic name is misspelled.

Pack 1—Marginellidae [and Cystiscidae]

28. *Prunum marginatum*: add "also occurs in the Caribbean" [CS2].
30. *Prunum olivaeforme*, not "*olivaeformis*" [Card 30/6192].
39. *Prunum guttatum*: "ranges in size from 15–25 mm., not 8 mm" [CS2].
47. *Volvarina inepta*: preoccupied name replaced by *Hyalina discors* (Roth) [Card 47/6190].
52. *Bullata matthewsi*, not "*mathewsi*" [CS19].
53. *Volvarina tenuilabra*: synonym of *Hyalina pallida* (Linné) [Card 53/6198].
60. *Volvarina rubella*: specimen is *V. cessaci* [Card 60/6195]; see Card 6183.
96. This number was skipped. Kaicher included, at least in some packs sold after the original publication date, a handwritten note about its absence.
97. *Granula pygmaea*: change genus to *Mesoginella* [Card 97/6194].
98. *Granula lavalleeana*, not "*lavaleeana*" [CS2, CS19]; specimen represents an undescribed *Gibberula* species [Cards 6189, 98/6197].

Pack 2—Muricidae

99. *Murex pecten*: change name to *M. pecten pecten* [Card 99/6040].
100. *Murex acanthostephes*: specimen is *M. scolopax* Dillwyn [Card 105/6048]; see Card 100/6047.
101. *Phyllonotus oculatus*, not "*oculus*" [CS3].
102. *Murex ternispina*: specimen is *M. spicatus* Ponder and Vokes [Card 6009]; see Card 102/6049.
105. *Murex scolopax*: specimen is *M. altispira* Ponder and Vokes [Card 6004].
106. *Murex troscheli*: reissued as Card 106/6052 with revised text.
107. *Murex unidentatus*: synonym of *M. trapa* Röding [Card 538/5050].
108. *Murex aduncospinosus*: reissued as Card 108/6041 with revised text.
111. *Murex coppingeri*: reissued as Card 111/6044 with minor changes to text.
114. *Murex brevispina*: change to *M. brevispina brevispina* [Card 114/6043].
126. *Murex macgillivrayi*: change to *M. brevispina macgillivrayi* [Card 120 [*sic*]/6046].
134. *Chicoreus fulvescens*: change genus to *Hexaplex* [CS10].
143. *Siratus antillarum*: specimen is *S. formosus* [Card 143/2575].
145. This number was skipped; assign to unnumbered *Chicoreus damicornis* [Note 1].
146. This number was skipped; assign to unnumbered *Chicoreus spectrum* [Note 1].
151. *Murex tribulus*: specimen is *M. falsitribulus* Ponder and Vokes [Card 6010]; see 151/6051.

Pack 3—Mitridae [and Costellariidae]

225. *Subcancilla flammea*: specimen is *Mitra intersculpta* Sowerby [ES5], i.e., *Ziba intersculpta* (Sowerby) [CS15]; see Card 225A/1529.
232. *Strigatella decurtata*, not "*decurta*" [CS19].
234. *Strigatella gausapata*, not "*gauspata*" [ES5].
245. *Costellaria michaui*: specimen is *C. deshayesii* (Reeve) [ES5]; specimen is *C. alauda* (Sowerby) [CS15]; see Cards 245A/1534, 1515, 1516.
261. *Pusia hanleyi*: identification questioned [CS15]; see Card 261A/1536.
266. *Costellaria styliola*: species was transferred to tentatively to *Latiromitra* (Turbinellidae) by Bouchet and Kantor (2000).
269. *Pusia sulcata*: specimen is *P. albocincta* (C. B. Adams) [ES5, CS15]; see Card 269A/1540.
271. *Pusia exigua*: specimen is *Costellaria sykesi* (Melvill) [CS15]; see Card 271A/1539.
284. *Costellaria pulchella*: adult illustrated on Card 284A/1532.
287. *Pusia hendersoni*: change genus to *Costellaria* [CS15]; see Card 287A/1538.
288. *Vexillum dennisoni*: "Delete *taylorianum* Sby from the synonymy . . . . The type of *taylorianum* is a juvenile of another species" [ES5].
290. *Zierliana woldemarii*, not "*woldermarii*" [ES5, CS19].

Pack 4—Mitridae [and Costellariidae]

345. Not issued, removed by Kaicher [ES4].
369. This number was skipped; assign to unnumbered *Pusia amabile* [*sic*, *amabilis*] [Note 1].
370. *Cancilla aegra*: specimen is *C. pia* (Dohrn) [CS15]; see Cards 370A/1533 and 1507.
385. *Strigatella auriculoides*: specimen is *S. assimilis* (Pease) [CS15]; see Cards 385A/1535 and 1438.

Pack 5—Strombidae

122. Add this number to the card for *Varicospira crispata* [CS6].
434. *Strombus gibberulus gibbosus*, not "*gibberulis*" [Note 3].
448. *Strombus gibberulus gibberulus*, not "*gibberulis*" [Note 3].
456. *Strombus gibberulus albus*, not "*gibberulis*" [Note 3].
466. Add this number to the card for *Lambis truncata* [CS6].

Pack 6—Muricidae

518. *Murex nigrospinosus*, specimen is *M. ternispina* Lamarck [Card 102/6049].
524. *Murex occa*: reissued as Card 524/6042 with minor changes to text
526. *Murex malabaricus*: see holotype on Card 526/2573.
538. *Murex trapa*: reissued as Card 538/6050 with revised text.
543. *Murex concinnus*: reissued as Card 543/6045 with revised text.
572. *Poirieria zelandica*, not "*Poireria*" [Note 7].
575. *Hexaplex densus*: specimen is *H. pudicus* [Card 575/2579]; see Card 2504.
584. *Favartia gravida*: preoccupied name replaced by *Favartia emersoni* Radwin and D'Attilio, 1976 [Card 584/2577].
591. *Homalocantha oxyacantha*, not "*oxyeantha*" [Note 3].

Pack 7—Terebridae

616. *Hastula lauta*: synonymy with *H. matheroniana* by Cernohorsky and Bratcher (1976) questioned. "*H. matheroniana* is considerably smaller than *H. lauta*, proportionally much narrower and has a much smaller protoconch" [CS13]. See Card 678.
658. *Terebra monile*: preoccupied name replaced by *Terebra quoygaimardi* Cernohorsky and Bratcher, 1976 [CS13].

Pack 8—Naticidae

726. *Naticarius brunneolinea*, not "*brunneolineus*" [Note 4].
739. *Tectonatica violacea*: change combination to *Natica violacea* (Sowerby) [Card 739A/3027].
744. This number was skipped; see 745 below [Note 1].
745. Two cards have this number, *Naticarius grayi* and *Euspira pallida*; one of them should have been 744, but it cannot be determined which.
773. *Tectonatica tecta*: change to *T. tecta* form *gemmana* (Reeve) [CS30]; see Card 2955.
779. *Euspira pulicaris*: change combination to *Natica pulicaris* Philippi, because of white calcareous operculum with three ridges [CS29].
792. *Sinum minus*, not "*minor*" [Note 6].

Pack 9—Mitridae [and Costellariidae]

824. *Costellaria laterculata*, syntypes do not match type illustration; use name *C. oriflavens* (Melvill) instead [CS12].
832. *Pusia emiliae*: specimen is *P. micra* (Pilsbry) [CS15]; see Cards 832A/1530 and 1514.
867. *Costellaria radix*: specimen is *C. obeliscus* (Reeve) [CS15]; see Cards 867A/1531 and 248.
873. *Mitra lienardi*: change to *M. ferruginea* form *lienardi* [CS15]; see Card 873A/1537.
900. *Pusia catenata*: better specimen illustrated on Card 900A/1528.

Pack 10—Volutidae

904. *Lyria kurodai*, not "*kurodae*" [Note 3].

Pack 11—Conidae

1058. *Conus havanensis*: "I now tend to agree with William Old that this is a synonym of *Conus magellanicus* Hwass"; see Card 1367 [CS14].

Pack 12—Conidae

1122. *Conus scitulus scitulus*: specimen is *C. algoensis algoensis* Sowerby [CS14].
1156. *Conus cinereus*: author is Hwass [CS19].
1194. *Conus kinoshitai*, not "*kinoshitae*" [Note 3].

Pack 13—Conidae

1248. *Conus zeylanicus*, not "*zelanicus*" [CS19].
1257. *Conus sphacelatus*, not "*sphacealatus*" [CS19].
1259. *Conus lineopunctatus*, change authorship to Kaicher [see above].
1261. *Conus cyanostoma*, not "*cyanostomus*" [CS19].
1282. *Conus locumtenens* Blumenbach, not "Blumenback" [CS19].
1293. *Conus alexandrinus*: specimen is *C. musivus* Trovao [CS14]; change authorship of *C. alexandrinus* to Kaicher [see above]; Paes-da Franca, not "Pais-da Franca" [herein].
1303. *Conus kintoki*: authors are Habe and Kosuge [CS14].
1311. *Conus lobitensis*: change authorship to Kaicher; is *Conus fuscolineatus* Sowerby [see above]; Paes-da Franca, not "Pais da Franca" [CS14].
1313. *Conus negroides*, change authorship to Kaicher [see above]; Paes-da Franca, not "Pais da Franca" [CS14].

Pack 14—Conidae

1328. This number was skipped between Packs 13 and 14 [CS15].
1342. *Conus classiarius*, not "*classarius*" [CS19].

Pack 15—Mitridae [and Costellariidae]

1498. *Pusia crocata*, not "*crocatum*" [CS19].
1526. This number was skipped, assign to unnumbered *Mitra carbonacea* [Note 1].

Pack 16—Muricidae

1540. This number was used in both Pack 15 (*Pusia albocincta*) and Pack 16 (*Boreotrophon alaskanus*) [CS19].
1542. This number was skipped [CS19].
1590. Specimen illustrated is not *Ocenebra aciculatus* [CS20], but *Pisania dorbignyi* (Payraudeau, 1826) [herein]; see Cards 1590A/2067 for *Ocinebrina aciculata* and 1343 for *Pisania dorbignyi*.
1640. *Evokesia rufonotata*: *Evokesia* misspelled in text [herein].

Pack 17—Cymatiidae

1655. *Cymatiella gaimardi*: synonym of *Sassia sexcostata* (Tate) [Card 1655/3337].
1659. *Cabestana spengleri*: change genus to *Cymatium* [Card 1659/3339].
1663. *Fusitriton laudandus*: change to *F. magellanicus laudandus* [Card 1663/3340].
1667. *Gyrineum gyrinum*, not "*gyrnium*" [CS19].
1671. *Cabestana doliarium*: author is Linné [CS19].
1692. *Septa aegrota*: this printed name changed to *Ranularia aegrota* by a self-adhesive label in packs mailed at time of publication. In many packs issued subsequently this card did not receive the corrective label [herein].
1699. ? *Monoplex lignarius*, not "*lignarium*" [Note 1]; probably a *Septa* [CS19].
1702. *Ranularia gutturnium*, not "*gutturnia*" [Note 4].
1703. *Fusitriton retiolus*: change to *F. magellanicus retiolus* [CS32].
1706. *Fusitriton murrayi*: change to *F. magellanicus murrayi* [CS32].
1707. *Monoplex parthenopeum parthenopeum*: change genus to *Cymatium* [Card 1707/3342].
1708. *Biplex jucunda*, not "*jacunda*"; magnification is ×2, not ×1 [CS19].
1717. *Fusitriton cancellatus*: synonym of *F. magellanicus magellanicus* (Röding) [CS32].
1726. "Protoconch differences suggest *Cabestana klenei* is a *Septa*" [CS19].
1731. *Negyrina subdistorta*: change genus to *Sassia* [Card 1731/3343].
1732. *Sassia semitorta*: change to *S. nassariformis semitorta* [Card 1732/3328].
1744. *Gutturnium lineatum*: change genus to *Cymatium* [Card 1744/3341].

Pack 18—Fasciolariidae

1754. *Fusinus leptorhynchus*, not "*leptorhyncus*" nor "*leptohyrncus*" as in CS46 [Note 3].
1757. *Latirus amplustre*, not "*amplustris*" [Note 4].
1766. *Granulifusus rufinodatus*, not "*rufinodis*" [CS46].
1768. *Granulifusus suboblitus*: change to *G. nipponicus suboblitus* [CS46].
1787. *Latirus mediamericanus*, not "*mediaamericanus*" [Note 3].
1790. *Latirus bairstowi*: change combination to *Dolicholatirus bairstowi* (Sowerby) [CS46].
1798. *Fusinus albinus*: see syntype on Card 1798/4721.
1800. *Dolicholatirus ernesti*: change combination to *Teralatirus ernesti* (Melvill) [ES18]
1815. *Fusinus nigrirostratus*: synonym of *F. tuberosus* (Reeve) [CS46].
1820. *Fusinus sandvichensis*, not "*sandwichensis*": see lectotype on Card 1820/4728. The name was spelled both ways by Sowerby, 1880, the original author, a first reviser's choice establishing the correct spelling was made by Snyder (2003).
1828. *Pleuroploca heynemanni*: change to *P. lugubris heynemanni* [CS46].
1836. *Microcolus dunkeri*: specimen is *M. lincolnensis* (Crosse and Fischer), which is not synonymous [Card 1836/4720]; see Card 4655.
1851. *Fusinus marensis*: change to *F. dilectus* (A. Adams) [Card 1851/4729].

Pack 19—Cancellariidae

1924. *Agatrix agassizii*: catalogue number is USNM 93711, not 73711 [herein].
1940. *Admete microscopica*: catalogue number is USNM 82977, not 32977 [herein].

Pack 20—Muricidae

1977. *Evokesia grayi*, not "*Evoksia*" [Note 7].
1983. *Trophon geversianum*, not "*gervesianus*" [Note 3].
1985. *Murex chrysostoma*, not "*chrysostomus*" [Note 4].
1989. *Ocinebrina purpuroidea*, not "*Ocenebrina*" [Note 7].
1998. ? *Ocinebrina suga*, not "*Ocenebrina*" [Note 7].
2005. *Attiliosa striata*: change name to *Attiliosa philippiana* (Dall), which is not synonymous [Card 2005/2574].
2009. This number was skipped [Note 1].
2010. *Risomurex schrammi*: specimen is *R. deformis* (Reeve) [Card 6066]; see Card 2010/6053.
2014. *Murexsul nothokieneri*, not "*nothokiener*" [Note 3].
2034. *Hexaplex canariensis*, not "*canariensus*" [Note 3].
2038. *Evokesia ferruginosa*, not "*Evoksia*" [Note 7].
2052. *Afritrophon insignis*: specimen with adult aperture shown on Card 2052/2576.
2060. *Ocenebra acanthopherus* Montrouzier: there is no such name; Houart (2001) considered it an error for *O. acanthophora* Monterosato, 1875, which is a nude name. Kaicher gave no description, so it remains a nude name [herein]. Houart (2001) identified Kaicher's illustrated specimen as *Ocinebrina hispidula* (Pallary, 1904).
1590A/2067. *Ocinebrina aciculata*, not "*Ocenebrina*" [Note 7].

Pack 21—Trochidae

2138. *Trochus satrapius*: author is von Martens, not "von Maltzan" [herein].
2167. *Calliostoma stenomphala*, not "*stenomphula*" [Note 3].
2177. *Calliostoma deceptum*, not "*decepulum*" [Note 3].

Pack 22—Trochidae

2178. This number was skipped between Packs 21 and 22 [Note 1].
2241. *Clanculus omalomphalus*, not "*omalomphorus*" [Note 3].
2242. *Calliostoma ormophorus*: change genus to *Clanculus* [CS30].
2275. Not issued; removed by Kaicher [CS22].

Pack 23—Epitoniidae

2285. *Epitonium alizonae*, not "*alizonum*" [Note 5].
2289. *Epitonium bulbulus*, not "*bulbulum*" [Note 4].
2292. *Epitonium clathrus*, not "*clathrum*" [Note 4].
2303. This number was skipped [ES23].
2320. *Epitonium helicornua*, not "*helicornuum*" [Note 4].
2325. *Epitonium macromphalus*, not "*macromphalum*" [Note 4]
2328. Add this number to unnumbered card for *Cirsotrema hidryma* [ES23].
2332. Add this number to unnumbered card for *Epitonium geniculatum* [ES23].
2333. *Epitonium melius*, not "*melior*" [Note 6].
2342. *Epitonium millecostatum*, not "*millecostum*" [Note 3].
2350. *Epitonium rarecosta*, not "*rarecostum*" [Note 4].
2358. *Amaea teramachii*: change authorship to Kaicher; is *Amaea sericogazea* Masahito, Kuroda and Habe [see above].

Pack 24—Thaididae

2448. *Azumamorula mutica*, not "*Azumorula*" [Note 7].
2457. *Morula iostomus*, not "*iostoma*" [Note 4].
2470. *Haustrum ventricosum*: change authorship to Kaicher; is *Dicathais orbita* Gmelin [see above].
2484. *Morula gemmulifera* (Pease): No such name was introduced by Pease. The specimen illustrated is conspecific with *Engina monilifera* Pease (1860), which is a synonym of *Morula echinata* (Reeve, 1846) according to Cernohorsky (1979). Therefore we consider "*gemmulifera*" to be a lapsus for "*monilifera*". The alternative is that, because the card contains a description, Kaicher had inadvertently validated a manuscript name of Pease based on a specimen label in a collection. We reject this possibility because Kaicher cited three locations indicating the geographic range of the species: "Samoa, Tahiti, Hawaii". If she had validated a manuscript name, in all likelihood she would have cited only a single locality.

Pack 25—Muricidae

2507. *Boreotrophon cepula*, not "*cepulus*" [Note 4].
2542. *Evokesia paucimaculata*, not "*Evoksia*" [Note 7].
2562. *Pterorytis hamatus*, not "*Pteroytis*" [Note 7].
2568. *Risomurex idosia*, not "*iodsia*" [Note 3].
2588. *Stramonitrophon longstaffi*, not "*Straminotrophon*" [Note 7].
2591. ? *Evokesia nitens*, not "*Evoksia*" [Note 7].

Pack 26—Marginellidae [and Cystiscidae]

2634. *Cystiscus aphanospira*, not "*aphanospera*" [Note 3]; Coovert (1999) erroneously changed it to "*aphanospirus*" [Note 4]; description should read "2 strong columellar folds (trace of smaller one)" [CS26].
2662. *Marginella diadochus*: locality should read "supposedly from Indian Ocean (Sunda Strait)." (This correction erroneously referred to Card 2709 on CS26) [CS28].
2676. *Glabella reeveana*, not "*reeviana*" [CS26].
2686. *Volvarina obscura*: specimen is misidentified and may represent an undescribed species [Card 2686/6191].
2687. Not issued; removed by Kaicher [CS26].
2709. See 2662 above.

Pack 27—Terebridae

2752. *Terebra delicatula*: change authorship to Kaicher; is *Terebra alba* Gray [see above].
2768. *Parviterebra separanda*: change family to Columbellidae [Card 2768/1247].
2797. *Parviterebra thyraea* Melvill, not "*thyrsaea* Melvin" [herein]; change family to Columbellidae [Card 2797/1248].

Pack 28—Haliotidae

2823. *Haliotis ovina*: specimen is *H. cyclobates* Peron [*sic*: Péron] [CS29].
2877. *Haliotis diversicolor*: misprinted as 2977 [herein].

Pack 29—Naticidae

2922. *Naticarius lineozona*, not "*lineozonus*" [Note 4].
2938. *Amauropsis moerchi*, not "*morchii*" [herein]; species transferred to Epitoniidae, as *Problitora moerchi*, by Wilson (1993).
2955. *Tectonatica tecta*: specimen matches the neotype [CS30]; see Card 773.
2958. *Neverita vestita*, not "*vastita*" [Note 3].
2959. *Eunaticina rhodocheila*, not "*rhodocheilus*" [Note 4].

2961. *Natica variolaria*: change authorship to Kaicher; is a *Notocochlis* [see above].
2980. *Amauropsis globulus*: species transferred to Epitoniidae, as *Problitora globula*, by Wilson (1993).
2990. Not issued; removed by Kaicher [ES29].
3013. *Natica insularum*: A postcard postmarked October 26, 1981 asked that this card be destroyed as the illustrated specimen was misidentified; however, the card was removed from some packs before they were shipped [ES29]. *Natica insularum* is correctly shown on Card 2998.

Pack 30—Epitoniidae

3049. *Epitonium acanthopleura*, not "*acanthoplerum*" [Note 3, 4].
3062. *Epitonium christyi*, not "*chrystyi*" [Note 3].
3070. *Epitonium platypleura*, not "*platypleurum*" [Note 4].
3103. *Epitonium labeo*, not "*labeum*" [Note 3].

Pack 31—Nassariidae

Pack cover card. *Nassarius consensus* is not sinistral; negative accidentally "flopped" [CS31].
3137. Two cards have this number. *Nassarius brunneostomus* [*sic*, *brunneostoma*] and *N. striatus* [Note 2].
3184. *Nassarius luteostoma*, not "*luteostomus*" [Note 4].
3214. This number was skipped [CS31].

Pack 32—Cymatiidae and Bursidae

3239 This number was skipped between Packs 31 and 32 [Note 1].
3288 Two cards have this number, *Bursa granularis cumingiana* and *Argobuccinum proditor*; one should have been 3289 but it cannot be determined which [Note 2].
3289 This number was skipped [Note 1]; see 3288 above.

Pack 33—Olividae

3346. This number was skipped between Packs 32 and 33 [Note 1].
3412. *Amalda novaezelandiae* form *bicolor* Angas: Angas did not introduce the name *bicolor*; it is a misspelling and misidentification of *tricolor* Gray, 1847 by Suter 1904 according to Olson (1956), who lists the name in the synonymy of *Baryspira novaezelandiae*. The illustrated specimen is also mislocalized, the species is endemic to New Zealand [herein].

Pack 34—Nassariidae

3458. *Nassarius mustelinus*: "the specimen illustrated, lower right, is the holotype (USNM 24200)" [CS34].
3482. *Nassarius abyssicola*, not "*abyssicolus*" [Note 4].
3525. *Nassarius cinctellus*: "the 'life-size' illustration is actually about twice life size" [CS34].
3536. *Nassarius leptospira*, not "*leptospirus*" [Note 4].

Pack 35—Epitoniidae

3570. *Epitonium echinatocosta*, not "*echinaticostum*" [Note 4].
3618. *Epitonium sericifila*, not "*sericifilum*" [Note 4].
3626. *Epitonium callipeplum*, not "*calipeplum*" [Note 3].
3637. *Epitonium foliaceicosta*, not "*foliaceicostum*" [Note 4].
3640. *Epitonium turritellula*, not "*turritellulum*" [Note 4].
3653. *Epitonium babylonia*, not "*babylonium*" [Note 4].

Pack 36—Cassidae and Oocorythidae [and Harpidae]

3730. *Morum sp.*: is *Morum ninomiyai* Emerson, 1986 [CS46].

Pack 37—Columbellidae

3770. This number was used in both Pack 36 (*Echinophoria carnosa*) and Pack 37 (*Anachis decimdentata*) [Note 2].
3778. *Anachis nisitella*: habitat previously unknown; matches shell illustrated as *Anachis catenata* from Puerto Rico in Caribbean Seashells by Warmke and Abbott (1961) [CS44].
3779. *Costoanachis fluctuata*, change genus to *Anachis* [ES37b].
3781. *Pseudanachis basedowi*, not "*Pseudoanachis*" [Note 7].
3812. *Mitrella livescens*: may be a *Euplica* [ES37a].
3822 *Columbella turturina*: change combination to *Euplica turturina* (Lamarck) [ES37a].
3825 *Columbella varians*: change combination to *Euplica varians* (Sowerby) [ES37a].
3863 *Columbella scripta*: change combination to *Euplica scripta* (Lamarck) [ES37a].

Pack 38—Columbellidae

3776–3875 These numbers were used in both Pack 37 and Pack 38 [CS39, Note 2].
3776. *Nodochila pascua* (Hertlein)
3777. *Mitrella denticulata* (Duclos).
3778 *Anachis cancellata* (Gaskoin)
3779 *Astyris perlucida* Dall.
3780. *Mitrella densilineata* (Carpenter)
3781. *Anachis cancellata* auct. *non* Gaskoin
3782. *Mitrella dartevillei* (Knudsen).
3783. *Anachis lightfooti* (E. A. Smith)
3784 *Astyris vidua* Dall.
3785. *Mitrella melvilli* (Knudsen).

3786. *Columbella castanea* Sowerby.
3787. *Cosmioconcha nitens* (C. B. Adams).
3788. *Anachis adelinae* (Tryon).
3789. *Anachis berryi* Shasky.
3790. *Anachis emergens* (Fischer-Piette and Nickles).
3791. *Anachis emergens* var.
3792. *Mitrella verdensis* (Knudsen).
3793. *Anachis atramentaria* (Sowerby).
3794. *Anachis consanguinea* (Sowerby).
3795. *Mitrella parvula* (Dunker).
3796. *Columbella paytensis* Lesson.
3797. *Mitrella mindorensis* (Reeve).
3798. *Anachis gaskoini* Carpenter.
3799. *Microcithara cithara* (Reeve).
3800. *Mitrella baccata* (Gaskoin).
3801. *Mitrella canariensis* (Orbigny).
3802. *Mitrella guttata* (Sowerby).
3803. *Mitrella xenia* Dall.
3804. *Mitrella essingtonensis* (Reeve).
3805. *Nassarina tehuantepecensis* (Shasky).
3806. *Mitrella tenuis* (Gaskoin).
3807. *Strombina paccana* Dall.
3808. *Mitrella australis* (Gaskoin).
3809. *Anachis descendens* (von Martens).
3810. *Mitrella delicata* (Reeve).
3811. *Nassarina cruentata* (Mörch).
3812. *Aesopus paucivolvis*: change combination to *Parviterebra paucivolvis* Pilsbry, since it is the type species of the genus, and the genus is recognized on Cards 2768 and 2797 (see above) [herein].
3813. *Mitrella vincta* Tate.
3814. *Mitrella loisae* Pitts and Kohl.
3815. *Mitrella dictua* (Tenison Woods).
3816. *Anachis incerta* (Stearns).
3817. *Anachis reedi* Bartsch.
3818. *Cosmioconcha palmeri* (Dall).
3819. *Nassarina helenae* Keen.
3820. ? *Euplica ucania* (Duclos).
3821. *Mitrella baculus* (Reeve).
3822. *Mitrella psilla* (Duclos).
3823. *Strombina edentula* Dall.
3824. *Anachis kirostra* (Duclos).
3825. *Anachis rugulosa* (Sowerby).
3826. ? *Pyrene yoldina* (Duclos).
3827. *Anachis* (s.l.) *iodostoma* (Gaskoin).
3828. *Zafrona pulchella* (Blainville).
3829. *Parametaria dupontii* (Kiener).
3830. *Strombina mendozana* Shasky.
3831. *Mitrella conspersa* (Gaskoin).
3832. *Mitrella pulla* (Gaskoin).
3833. *Astyris appressa* Dall.
3834. *Astyris projecta* Dall.
3835. *Mitrella venulata* (Sowerby).
3836. *Astyris multilineata* Dall.
3837. *Mitrella buccinoidea* (Sowerby).
3838. *Anachis lentiginosa* (Hinds).
3839. *Astyris rosacea* Gould.
3840. *Aesopus algoensis* (Sowerby).
3841. ? *Pyrene ida* (Duclos).
3842. *Anachis albella* (C. B. Adams).
3843. *Mitrella pyramidalis* (Sowerby).
3844. "*Pyrene*" *kincaidi* Tomlin.
3845. *Anachis leptalea* (E. A. Smith).
3846. *Mitrella apicata* (E. A. Smith).
3847. *Mitrella shepstonensis* (E. A. Smith).
3848. *Anachis obesa* (C. B. Adams).
3849. *Nassarina bushiae* (Dall).
3850. *Amphissa reticulata* Dall.
3851. *Euplica bidentata* (Menke).
3852. *Astyris amiantis* Dall.
3853. *Zafrona nebulosa* (Gould).
3854. *Mitrella sanctaehelenae* E. A. Smith.
3855. *Aesopus chrysaloidea* (Carpenter).
3856. *Aesopus hilum* (Hedley), not "*hilium*" [Note 3].
3857. *Aesopus cassandra* (Hedley).
3858. *Mitrella yorkensis* (Crosse).
3859. *Nassarina plexa* (Hedley).
3860. *Aesopus pallidulus* (Hedley).
3861. *Mitrella russelli* (Brazier).
3862. *Anachis kraussii* (Sowerby).
3863. *Zafra divaricata* (Pilsbry).
3864. *Zafra alternata* (Gould).
3865. *Zetekia gemmulosa* (C. B. Adams).
3866. *Aesopus stearnsii* (Tryon).
3867. *Zafrona consobrina* Rehder.
3868. ? *Zafrona retiaria* (Tomlin), not "*retiara*" [Note 3].
3869. *Anachis burnupi* (E. A. Smith).
3870. *Ruthia mazatlanica* Shasky.
3871. *Mitrella baileyi* Bartsch and Rehder.
3872. *Anachis fusidens* Dall.
3873. *Aesopus japonicus* Gould.
3874. *Anachis meta* (Thiele).
3875. *Parametaria macrostoma* (Reeve).

Pack 39—Turridae

3892. *Cochlespira radiata*: specimen is not USNM 421774 but probably ANSP 300563; see Card 3907 [herein].
3907. *Cochlespira elegans*: catalogue number 421774 visible on shell is a USNM, not an ANSP, number; see Card 3892 [herein].
3939. *Agathotoma castellata*, not "*costellata*" [Note 3].

Pack 40—Coralliophilidae

4001. "*Coralliophila*" *kochiana*: change combination to *Lataxiena kochiana*; change family to Muricidae [Card 4001-6054]. See also Buccinidae 4001, below.
4080. "*Coralliophila*" *mansfieldi*: magnifications are "×2 and ×4" [ES40].

Pack 41—Nassariidae

4103. *Nassarius sinarum*, not "*sinarus*" [Note 5].
4117. *Bullia indusica*, not "*indusindica*" [Note 3].

4148. *Cyllene unimaculata*, not "*unimacylata*" [ES41].
4185. *Bullia otaheitensis*, not "*othaeitensis*" [ES41].

Pack 42—Columbellidae

4205. *Aesopus spicula*, not "*spiculum*" [Note 4].
4210. *Pyrene ogasawarana*: removed from Pack 42, reprinted and shipped with Pack 43 [ES42a].
2768/4247. *Parviterebra separanda*, not "*separtanda*" [Note 3]; author is Tomlin, not Melvill [herein].
2797/4248. *Parviterebra thyraea* Melvill, not "*thyrsaea* Melvin" [Note 3].
4297. *Mitrella phylina*: removed from Pack 42, reprinted and shipped with Pack 43 [ES42a]. Other cards that were reprinted, but not first removed are 4211–4216, 4218–4220, 4225, 4273, 4276, 4292, 4294, 4296, 4299, 4304, 4305.

Pack 43—Buccinidae

4004. *Nassaria pusilla* form *laevior*: misprint for 4404 [herein].
4310. *Babylonia canaliculata*: change to *B. spirata valentiana* (Swainson) [Card 4935/4310].
4339. *Neptunea antiqua*: specimen is *N. despecta despecta* (Linné) [CS45].
4343. *Pisania dorbignyi* Payraudeau: not "Payrandeau" [herein].
4345. *Buccinum leucostoma*, not "*leucostomum*" [Note 4].
4356. *Buccinulum linea linea*, not "*lineum*" [Note 4].
4369. *Phos cyanostoma*, not "*cyanostomus*" [Note 4].
4373. *Cantharus melanostoma*, not "*melanstomus*" [Note 4].
4383. *Cantharus erythrostoma*, not "*erythrostomus*" [Note 4].
4397. "*Cantharus*" *dentatus*: change combination to *Eosipho dentatus* (Schepman) [Card 4941/4397].
4404. See 4004.

Pack 44—Buccinidae

4417. *Metula elena*: magnifications ×2 and ×4, not ×1 and ×2 [Card 4936/4417].
4440. *Pollia pastinaca*, not "*pastinacea*" [Note 3].
4460. *Clivipollia pulchra*: change genus to *Engina* [Card 4460/5833].
4470. *Searlesia dira*, not "*Searlsia*" [Note 7].
4513. *Cantharus albozonatus*: author is Kosuge, not "Kosuge and Habe" [herein]; preoccupied name replaced by *C. leucotaeniatus* Kosuge, 1985 [Card 4513/5835].

Pack 45—Trochidae

4526. *Clanculus berthelotii*, not "*bertheleti*" [Note 3].
4614. *Calliostoma vincentae*, change authorship to Kaicher; probable synonym of *Callumbonella suturalis* Philippi [see above].

Pack 46—Fasciolariidae

4629. *Latirus rhodostoma*, not "*rhodostomus* [Note 4].
4651. *Latirus croceus*, not "*crocatus*" [Note 3].
4655. *Microcolus lincolnensis*: *M. dunkeri* mentioned in text is Card 4720, not 4719 [herein].
4665. *Latirus singularis*, not "*cingularis*" [Note 3].
4671. *Latirus elegans*: author is A. Adams, not "(Gray)" [herein].
4674. *Latirus mannophorus*, not "*mannophophorus*" [Note 3].
4680. *Leucozonia ocellata*, not "*ocellifera*" [Note 3].
4694. *Fusinus fragilissimus*: change genus to *Bayerius*, change family to Buccinidae [Card 4694/5834].
4710. *Latirus luculentus*: change combination to *Godfreyana luculenta* (A. Adams), change family to Buccinidae [Card 4710/5832].
4711. *Fusinus rufocaudatus*: change genus to *Exilioidea*, change family to Turbinellidae [CS55]; reissued as Card 5628.
4715. *Pleuroploca lignarius*, not "*lignaria*" [Note 4]; originally spelled "*ligniarius*" by Linné (1758), but as "*lignarius*" by Linné 1767. Vokes (1971) noted that the latter was correct Latin, but retained the spelling *ligniarius* in accordance with the ICZN rules then in effect. As the later spelling *lignarius* has remained in prevailing use, attributed to Linné, 1758, it is to be maintained (ICZN Art. 33.3.1) [herein].

Pack 47—Neritidae

4733. *Dostia lecontei*, not "*leconti*" [Note 3].
4750 *Clypeolum subauriculatum*, not "*subauritulatum*" [Note 3].
4756. *Clypeolum tahitensis*: change *N. auriculata* in text to *C. auriculatum* [herein].
4765. *Theodoxus elongatulus*, not "*elongatus*" [Note 3].
4773. *Theodoxus guadianensis valentina*: author is Graells, not "Graello" [herein].
4779. *Theodoxus peloponensis*, not "*peloponnesius*" [Note 3].
4787. *Nerita birmanica*: author is Troschel, 1878, not Recluz [herein].
4824. *Neritina vespertina*: change genus to *Clypeolum*, to agree with placement of *C. tahitensis* (Card 4756), with which it is compared [herein].

Pack 48—Buccinidae

4851. *Metula sp.*: is *M. africana* Bouchet, 1988 [Card 4851/5888].
4862 *Cantharus leucozonum*, not "*leucozonus*" [Note 4].
4885 *Pisania herrmannseni*, not "*hermanseni*" [Note 3]; A. Adams (1855) spelled the name "*hermannseni*", stating "We have named it after M. Hermannsen, who has contributed so materially towards the natural history of the Mollusca, by his

valuable work on Bibliography and Synonyms". Because it is clear that Adams' intention was to name the species for A. N. Herrmannsen, author of *Indicis Generum Malacozoorum Primordia* (1846–1852), the spelling must be corrected to "*herrmannseni*" under ICZN Article 32.5.1.

4899. *Buccinum kinukatsugi*, not "*kinokatsuge*" [Note 3].

4900. *Prodotia iostoma*: change name to *Prodotia* sp. "A" [Card 4900/5831], wrong protoconch illustrated; see Cards 5826 and 5846 for *P. iostoma* and 5858 for *P.* cf. *P. iostoma*.

Pack 49—Olividae

4994. *Olivella formicacorsii*, not "*formicacorsi*" [Note 3; named for Dr. A. Formica Corsi].

5031. *Olivella guildingi*: type locality is St. Vincent [ES49a].

5036. *Olivella nivea*: specimen is from Espirito Santo, Brazil; wrong protoconch illustrated [ES49a].

5047. Not issued, removed by Kaicher [ES49b].

Pack 50—Trochidae

5053. *Cantharidella tessellata*: compare to syntype shown on Card 5791/5053; see Card 5712.

5067. *Bathybembix aeola*: specimen is *B.* cf. *aeola* [Card 5687/5067]; see Card 5688.

5080. *Micrelenchus sanguineus sanguineus*, not "*Michrelenchus*" [Note 7].

5095. *Minolia holdsworthana*: authorship is Nevill and Nevill, not "Nevill" [herein].

5120. *Micrelenchus tenebrosus*, not "*Michrelenchus*" [Note 7].

5123. *Micrelenchus sanguineus cryptus*, not "*Michrelenchus*" [Note 7].

5147. *Micrelenchus rufozona*, not "*Michrelenchus rufozonus*" [Notes 3, 6].

5149. *Micrelenchus dilatatus*, not "*Michrelenchus*" [Note 7].

5152. *Astele pulcherrimus*: synonym of *Coralastele punctocostatus* [Card 5686/5152].

Pack 51—Olividae

5253. Two cards have this number, *Oliva* cf. *aniomina* and *O. arctata* [Note 2].

5259. This number was skipped [Note 1].

Pack 52—Turbinidae

5317. *Guildfordia triumphans*, not "*Guilfordia*" [Note 7].

5320. *Guildfordia yoka*, not "*Guilfordia*" [Note 7].

5323. *Micrastraea rutidoloma*, not "*rutidiloma*" [Note 3].

5326. *Guildfordia aculeata*, not "*Guilfordia*" [Note 7].

5329. *Guildfordia monilifera*, not "*Guilfordia*" [Note 7].

Pack 53—Fissurellidae

5381. *Medusafissurella salebrosa*: "type species of *Medusafissurella*" [CS53].

5411. *Dendrofissurella scutellum*: "type species of *Dendrofissurella*" [CS53].

5420. *Diodora elizabethae*, not "*elixabethae*" [Note 3].

5437. This number was skipped; assign to unnumbered *Diodora calyculata* [Note 1].

5451. *Fissurella pulchra*: not that species; identity not determined [CS54].

Pack 54—Olividae

5502. *Oliva miniacea*, not "*mineacea*" [Note 3].

Pack 55—Turbinellidae

5660. This number was skipped [Note 1].

5661. This number was skipped [Note 1].

Pack 56—Trochidae

5686/5067. *Coralastele punctocostatus*, number should be 5686/5152 [herein]; see next item and 5152 above.

5687/5152. *Bathybembix* cf. *aeola*: number should be 5687/5067 [herein]; see previous item and 5067 above.

5712. *Cantharidella tessellata*, not "*tesselata*" [Note 3].

5716. *Rossiteria nucleus*, not "*nuclea*" [Note 4].

5721. "*Minolia*" *holdsworthana*: authorship is Nevill and Nevill, not "Nevill" [herein].

5757. Not issued; removed by Kaicher [CS56].

5791/5053. *Cantharidella tessellata*, not "*tesselata*" [Note 3].

Pack 57—Buccinidae

5795. *Crassicantharus norfolkensis*: size is about 10 mm, not "40+ mm" [herein].

5819. *Searlesia fuscolabiata*, not "*Searlsia*" [Note 7].

5833. *Engina pulchra*: note catalog number is 1966608 not 196608 on original card (4160) [herein].

5842. This number was skipped, assign to unnumbered *Colubraria tortuosa* [Note 1].

5848. *Colubraria bayeri*: transferred to *Tritonoharpa* (Cancellariidae) by Harasewych, Petit and Verhecken (1992).

Pack 58—Ovulidae

5914. *Cyphoma signatum*, museum number is USNM 599386 [ES58].

5920. *Galera aenigma*, change genus to *Galerovolva* [ES58].

5926. *Pseudocypraea exquisita*: in text discussion, change *P. adamsi* to *P. adamsonii* [ES58].

5943. *Spiculata barbarensis*: change "Dall" to "(Dall)" [ES58].

5944. *Phenacovolva bartschi*: museum number is USNM 429178 [ES58].
5951. *Xandarovula formosana*: change "Azuma" to "(Azuma)" [ES58].
5955. *Phenacovolva loebbeckeana*: museum number is USNM 219894 [ES58].
5964. *Primovula rutherfordiana* Cate, not "(Cate)" [ES58].
5965. *Habuprionovolva choshiensis*, not "*Habuiprionovolva*" [ES58].
5968. *Phenacovolva wakayamaensis*: specimen is *P. yoshioi* (Azuma and Cate) [CS59].
5970. *Phenacovolva clenchi*: museum number is USNM 282618 [ES58].
5971. *Hiatavolva depressa*, not "*Hiatovolva*" [ES58].
5985. *Cyphoma mcgintyi*, not "*macgintyi*" [ES58].
5986. *Crenavolva serrula*: museum number is USNM 735736 [ES58].
5988. *Pseudosimnia sphoni*: specimen figured is the holotype [ES58].
5989. *Crenavolva "striatula" tinctura*: museum number is AMS C.64070 [ES58].
5992. *Stohleroma fumikoae*: change "Azuma and Cate" to "(Azuma and Cate)" [ES58].
5999 *Simnialena uniplicata*: museum number is USNM 590065 [ES58].
6000. *Lacrima simulans*: museum number is USNM 284921 [ES58].

Pack 59—Muricidae

6004–6052: Magnification, omitted from many *Murex* s.s. cards, is ×1 [CS59].
6007. (?) *Pygmaepterys aliciae*, not "*Pygmaeapterys*". Unnumbered *Poirieria kopua* erroneously assigned to this number on CS59; on some copies of CS59, Kaicher crossed out 6007 and wrote in 6038, which see.
6016. *Poirieria primanova*, not "*Poiriera*" [Note 7].
6017. *Pygmaepterys adensis*, not "*Pygmaeapterys*" [Note 7].
6038. This number was skipped; assign to unnumbered *Poirieria kopua* [Note 1]; see 6007 above.
6098. *Pygmaepterys richardbinghami*, not "*Pygmaeapterys*" [Note 7].
6070 This number was skipped; assign to unnumbered *Risomurex withrowi* [CS59].
6096. *Typhis occlusus*, not "*occulusus*" [Note 3].

Pack 60—Marginellidae [and Cystiscidae]

6108. *Homalocantha dovpeledi*, not "*Homalacantha*" [Note 7]
6111. *Canalispira attentia*, not "*Canalspira*" [Note 7].
6130. *Dentimargo smithii*: museum number is MCZ 207389, switched with Card 6171 (see below) [herein].
6141. ? *Prunum pyrulum*: change genus to ? *Persicula* [CS60].
6171. *Dentimargo idiochila*: museum number is ANSP 219511, switched with Card 6130 (see above); Coovert (1999) erroneously changed the ending to agree with *Dentimargo* [Note 4].
6185. *Canalispira replicata*, not "*Canalspira*" [Note 7].
6189. Two cards have this number: *Gibberula lavalleeana* of authors and *Volvarina perrieri* [Note 2].
6193. This number was skipped [Note 1].
6204. *Canalispira minor*, not "*Canalspira*" [Note 4].

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Reproduction of *Crepidula navicula* Mørch, 1877 and *Crepidula aplysioides* Reeve, 1859 (Caenogastropoda) from Morrocoy and La Restinga Lagoon, Venezuela

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ABSTRACT

Brooding specimens of *Crepidula aplysioides* and *Crepidula navicula* were collected from La Restinga Lagoon, Margarita Island and Las Luisas Bay, Morrocoy, Venezuela at a depth of 0.5–1 m. Individuals of *C. aplysioides* were attached to mangrove oysters and mussels that were attached to the roots of *Rhizophora mangle*, while those of *C. navicula* were attached to the gastropod *Modulus modulus*.

Brooding females of *C. aplysioides* measured 9.4–18.2 mm shell length and each female brooded 23.4 ± 4.5 egg capsules. The egg capsules had a triangular shape, with one corner extending to form a stalk that attached the egg capsule to the substrate. The capsule walls were thin and transparent. Egg capsules measured 0.5–2.1 mm length (without the stalk), 0.7–2.7 mm width, and the stalk 0.6–3.3 mm length. The number of eggs per capsule varied from 3 to 18. The uncleaved egg measured about 300 µm and all eggs developed. Nurse eggs were not observed. Cannibalism, however, was observed among sibling embryos and the number of hatchlings was significantly lower (by one individual) than the number of eggs. Hatching occurred as crawling juveniles measuring about 600 µm in shell length.

Brooding females of *C. navicula* measured 4.9–7.4 mm shell length and each female brooded 8.5 ± 2.2 egg capsules. The egg capsules were very similar to those of *C. aplysioides* but smaller (between 0.5 and 1.3 mm lengthwise) and contained 3–6 eggs each. The uncleaved eggs measured around 330 µm. All eggs develop, cannibalism was observed and the number of hatchlings was significantly lower than the number of eggs. Between 2–4 individuals hatched per capsule as pediveligers measuring 550–1172 µm shell length.

Female size determined fecundity, in terms of juvenile production, on both species. This is accomplished through two different strategies, the first an increase in the number of hatchlings per female at larger female sizes (*C. aplysioides*) and the second that larger females produced larger egg capsules with more hatchlings (*C. navicula*).

INTRODUCTION

The shells of *Crepidula* Lamarck, 1799 are limpet-like, flat or cap shaped, with a coiled apex at the posterior end, the interior has a shelly platform which is attached to the shell by both sides and covers about half of the internal area (the posterior portion of the soft body), and they have no operculum (Abbott, 1974; Díaz and Puyana, 1994).

Calyptraeids in the genus *Crepidula* are very common throughout the North and South American coasts both in the Pacific and the Atlantic. Abbott (1974) reported 13 species from North America, and Hoagland (1986) reported other additional six species. In the Caribbean, Díaz and Puyana (1994) and De Jong and Coomans (1988) reported 3 species from Colombia, the West Indies, Aruba, Curaçao, and Bonaire; these are *Crepidula aculeata* Gmelin, 1791, *Crepidula convexa* Say, 1822, and *Crepidula plana* Say, 1822. Warmke and Abbott (1961) reported three other species for the Caribbean, *Crepidula glauca* Say, 1822, *Crepidula protea* d'Orbigny, 1845, and *Crepidula riisei* Dunker, 1877. The taxonomic allocation of species is difficult solely on the basis of conchological characters given the impressive plasticity that these shells have when growing on different substrates. Hoagland (1986) made an advance in the systematics of the genus through the study of egg capsules, larval development, electrophoresis, and anatomy. Collin (2000a) stated that the taxonomy of the species of *Crepidula* with pale, flattened, concave, or recurved shells is particularly difficult and uncertain; she separated the *Crepidula plana* complex from North America into three different species based on morphological, developmental, and molecular (mitochondrial cytochrome oxidase I) data.

Information regarding reproductive patterns of some species has proved to be very helpful in determining the

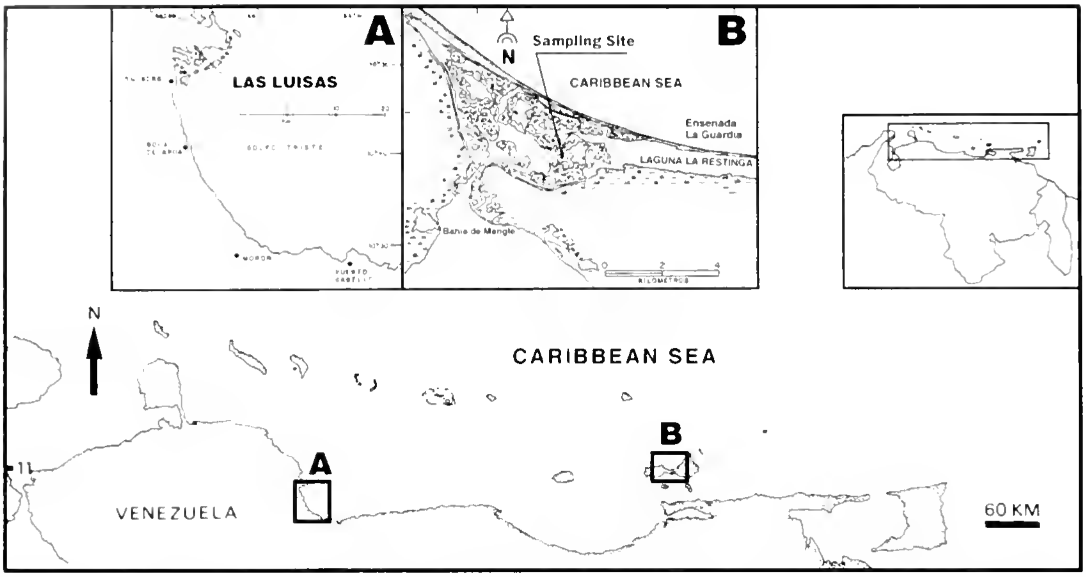


Figure 1. Map of the Caribbean showing collecting sites: (A) Las Luisas, Morrocoy National Park and (B) La Restinga Lagoon, Margarita Island.

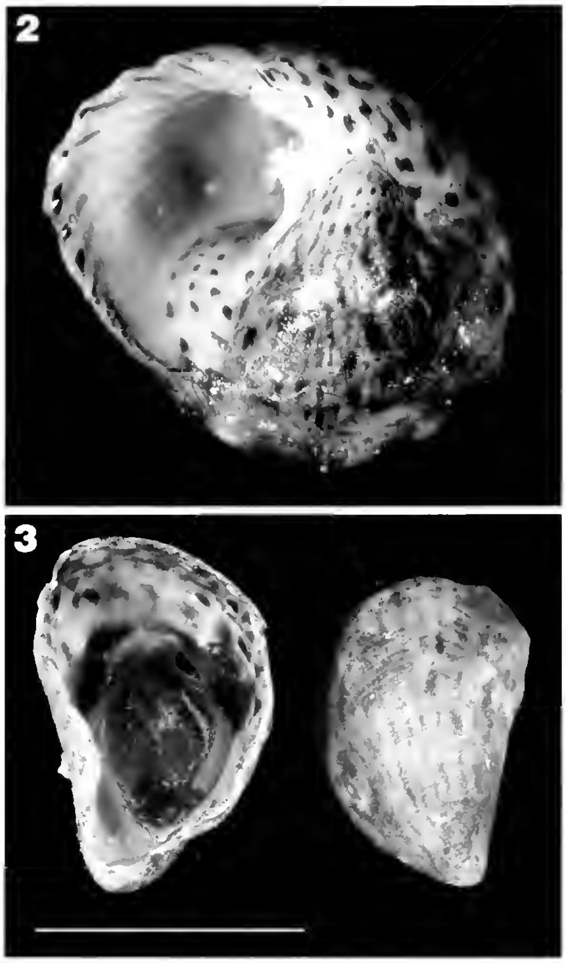
systematic placement of these species (Penchaszadeh, 1988). The major review of brood characteristics for Calyptraeidae included 19 *Crepidula* species (Hoagland, 1986) of which two species, *C. plana* Say, 1822 and *C. convexa* Say, 1822 had different data depending on geographic locality. In summary, as are all calyptraeids, *Crepidula* species are protandric hermaphrodites. They may have small or large lecithotrophic eggs, and as extra-embryonic food sources they may feed on nurse eggs or cannibalize sibling embryos. In consequence, developmental modes are variable and hatching can take place as planktotrophic veligers, pediveligers, or crawling juveniles. Cledón and Penchaszadeh (2001) described the reproduction of *Crepidula argentina* Simone, Pastorino and Penchaszadeh, 2000, and also gave a review of some of the reproductive characteristics of South American *Crepidula* species. Other studies describing the reproductive biology of several *Crepidula* species are: Knudsen (1950), Bandel (1976), Stone Ament (1979), Chaparro et al. (1999), Gallardo (1977, 1996) and Collin (2000a, b).

Herein, we describe the egg capsules, intracapsular development of the embryos, and hatching mode of two *Crepidula* species from Venezuela: *C. navicula* from Morrocoy National Park, which is located on the northwestern coast of Golfo Triste, and *C. aplysioides* from Isla de Margarita, an island located approximately 40 km north from the Araya Peninsula at the northeastern coast of Venezuela. The relationship between female size and the number and size of egg capsules, size of the eggs, and size of hatchlings was also determined as well as the relationship between capsule size and the number of eggs, embryos, and hatchlings contained therein.

MATERIALS AND METHODS

SPECIMENS

Crepidula navicula: specimens brooding egg capsules were collected in February 1995, September 1996 and February 2002 at Las Luisas, Morrocoy National Park, Falcón State (10°52′ N, 69°16′ W, Figure 1), at 0.2–1.0 m depth. The habitat consists of a turtle grass bed with some patches of sand and the calcareous alga *Halimeda monile* (Ellis and Solander) Lamour. The specimens were found attached to live *Modulus modulus* Linnaeus, 1758 (Figure 2), gastropods that were living on leaves of the turtle grass *Thalassia testudinum* Banks ex-Köning. The females (Figure 3) and egg capsules collected were observed live. To observe the embryos in the egg capsules during development, the female was carefully removed from the substrate and the underlying brood was observed under the stereoscopic microscope. After the observations, the female was reattached to its brood. This reattachment was usually successful, but when not, the embryos inside the egg capsules remained live for 8 days without the protection of the mother. In addition, we placed microscope slides inside the aquaria and some females spawned using these surfaces to attach their broods, allowing us to observe the egg capsules through the glass without removing the mother. Egg capsules at the different stages of development were fixed in a glucamine-acetate (GA) buffer containing 1–6% formalin (Miloslavich and Penchaszadeh, 1997) for at least 24 hours and preserved in ethanol. The photographs were taken from live material. Voucher material consisting of the entire adult individuals preserved in ethanol was deposited in the Field Museum of Natural History, Chi-



Figures 2–3. *Crepidula navicula* **2.** Ventral view of the gastropod host *Modulus modulus* with one individual of *C. navicula* attached. **3.** Ventral and dorsal view of *C. navicula* Scale bar = 10 mm.

Figures 4–5. *Crepidula aplysioides* **4.** Valve of host *Perna viridis* with one individual of *C. aplysioides* attached **5.** Ventral and dorsal view of *C. aplysioides* Scale bar = 10 mm

cago, FMNH 293349 and at the Museum of Comparative Zoology, Cambridge, MCZ 304129.

Crepidula aplysioides Brooding specimens were collected in February 2000 and October 2001 and 2002 at La Restinga Lagoon (located between 64°2′ W and 64°12′ W, 10°90′ N and 11°2′ N, Figure 1), Margarita Island, Nueva Esparta State, Venezuela. During the first field trip (February 2000), individuals were found attached to the mangrove oyster *Crassostrea rhizophorae* Guilding, 1828, that was attached to mangrove roots of *Rhizophora mangle* Linnaeus at a depth of 0.5–1.0 m. During the second field trip (October 2001), most of the animals had changed their substrate and were now attached to the invading mussel *Perna viridis* Linnaeus, 1758 (Figure 4) which had been previously reported in the Venezuelan Caribbean but not at this site (Penchaszadeh and Vélez, 1995). The females (Figure 5) and egg capsules were observed live as previously described for *C. navicula* and posteriorly were fixed and preserved in ethanol. Voucher material consisting of the entire individuals preserved in ethanol was deposited in the Field Museum of Natural History, FMNH 293348 and at the Museum of Comparative Zoology, MCZ 304130, 304131, 304132 and 304133.

Development

A total of 40 brooding females of *C. navicula* and 45 of *C. aplysioides* were collected. The following aspects of the spawn were studied: (1) number and size of egg capsules brooded per female, (2) number and size of eggs and developing embryos within the capsule, (3) observation of the different stages of development, and (4) hatching mode and size of hatchling. We studied the relationship between female size and number and size of capsules, and number and size of eggs, embryos and hatchlings per capsule as well as the relationship between capsule size and number and size of eggs and hatchlings per capsule using a Pearson product-moment correlation. Given that some samples may not be independent as they come from the same female, we calculated partial Pearson correlations using, when appli-

Table 1. Length, width and height of brooding females of *Crepidula naviculla* and *Crepidula aplysioides*. Results are reported as mean ± SD. Numbers in parenthesis indicate range (minimal and maximal values).

	Length (mm)	Width (mm)	Height (mm)
Crepidula navicula	5.9 ± 0.6 (4.9–7.1) n = 40	4.2 ± 0.4 (3.3–4.8) n = 40	2.2 ± 0.3 (1.7–2.7) n = 40
Crepidula aplysioides	12.4 ± 0.2 (9.4–18.2) n = 72	8.8 ± 1.4 (7.2–12.2) n = 72	3.0 ± 0.7 (2.8–3.9) n = 72

cable, the variables female volume, capsule area and number of capsules as controlling factors.

Given the growth particularities of the shells of *Crepidula* in relation to their susbstrate, instead of considering female size as shell length exclusively, we report female size as the volume of a half spheroid in which the volume is calculated by the following equation:

V (half spheroid) $= (4/3\ \pi\ .h.r1.r2)/2$, in which h = shell height, $r1$ = radius 1 (half shell length) and $r2$ = radius 2 (half shell width).

All observations of live and preserved material were carried out with a Zeiss stereoscopic microscope and Zeiss microscope; measurements were performed with an ocular micrometer.

RESULTS

SEXUAL MATURITY AND FEMALE SIZE—SPAWN RELATIONSHIPS

The shells of brooding females of *C. navicula* measured 4.9–7.1 mm length, 3.3–4.8 mm width, and 1.7–2.7 mm height (Table 1). The female genital papilla was observed in individuals larger than 3.5 mm shell length, while males (with presence of a penis) measured up to 5 mm shell length. Female volume of *C. navicula* was significantly correlated with capsule area (Pearson product moment correlation: $p < 0.001$). No correlation was observed between female volume and the other reproductive parameters. However, a relatively good correlation was found with hatching size ($p = 0.058$). Capsule area was correlated to number of eggs ($p = 0.004$), number of developing embryos ($p < 0.001$) and number of hatchlings per capsule ($p = 0.001$) (Table 2, Figure 6).

The shells of brooding females of *C. aplysioides* measured 9.4–18.2 mm length, 7.1–1.2 mm width and 2.8–3.9 mm height (Table 1). The female genital papilla was observed in individuals larger than 7.5 mm shell length, while males (with presence of a penis) measured up to 11 mm shell length. In this latter species we observed a significant relationship between female volume and number of capsules ($p = 0.002$), number of eggs per capsule ($p < 0.001$), number of embryos per capsule ($p < 0.001$), and number of hatchlings per capsule ($p < 0.001$). No relationship was observed between female

Table 2. Statistic results of female size–spawn relationships for *Crepidula navicula*.

Variables	r correlation	P	n	Controlled by
Female volume–number of capsules	0.139	0.394	40	None
Female volume–capsule area	0.396	0.001	157	Number of capsules
Female volume–number of eggs per capsule	0.199	0.444	18	Capsule area
Female volume–number of embryos per capsule	0.009	0.912	157	Capsule area
Female volume–number of hatchlings per capsule	0.051	0.826	22	Capsule area
Female volume–egg size	0.02	0.999	75	Number of capsules
Female volume–hatching size	0.248	0.058	61	Number of capsules
Capsule area–number of eggs per capsule	0.655	0.004	18	Capsule area Female volume
Capsule area–number of embryos per capsule	0.577	0.001	157	Female volume
Capsule area–number of hatchlings per capsule	0.652	0.001	22	Female volume
Capsule area–egg size	0.131	0.268	75	Female volume
Capsule area–hatching size	0.245	0.061	61	Female volume Number of capsules
Number of capsules–hatching size	0.519	0.001	61	Female volume
Number of hatchling per capsule–hatching size	0.135	0.001	61	Female volume

Pearson product-moment correlation.

Partial Pearson correlation using as controlling factor(s) the variable(s) which showed a significant correlation and controlling by female volume.

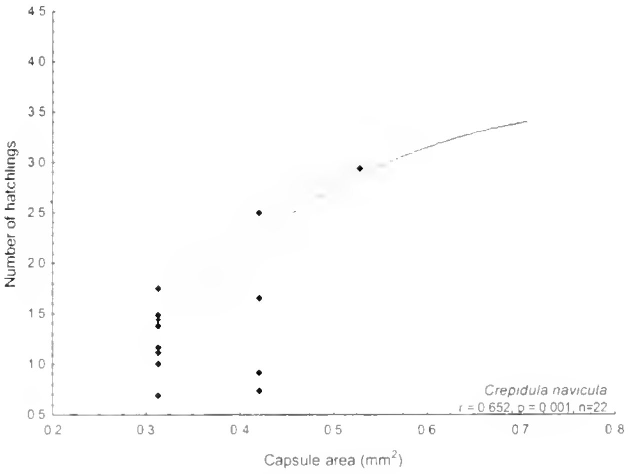


Figure 6. Relationship between number of hatchlings and capsule area of *Crepidula navicula*.

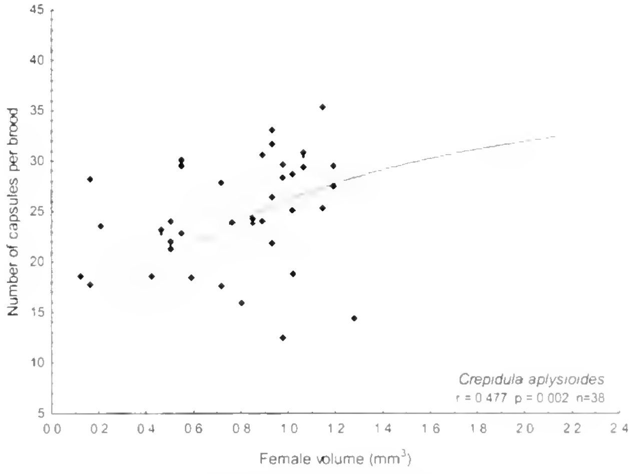


Figure 7. Relationship between female size (volume) and number of capsules per brood of *Crepidula aplysioides*.

size and hatchling size. Capsule area was correlated to number of developing embryos ($p < 0.001$) and number of hatchlings per capsule ($p < 0.001$). (Table 3, Figures 7, 8).

DEVELOPMENT

Crepidula navicula: The females brooded 5–15 egg capsules in the mantle cavity. The egg capsules measured 0.8–1.6 mm width and 0.5–1.3 mm length (from the base of the capsule to the tip), the stalk is thread-like and measures 1.0–1.2 mm length (Table 4).

The number of eggs per capsule varied from 1 to 6 (mean = 3 ± 1, n = 157). The uncleaved eggs were yellow and measured approximately 330 µm in diameter (Figure 9, Table 3). All the eggs developed, gastrulation is by epiboly as the micromeres at the animal pole divide

Table 3. Statistic results of female size–spawn relationships for *Crepidula aplysioides*.

Variables	r correlation	P (*)	n	Controlled by (**)
Female volume—number of capsules	0.4767	0.002	38	None
Female volume—capsule area	0.2395	0.153	38	Number of capsules
Female volume—number of eggs per capsule	0.4941	< 0.001	57	Capsule area Number of capsules
Female volume—number of embryos per capsule	0.728	< 0.001	70	Capsule area Number of capsules
Female volume—number of hatchlings per capsule	0.8705	< 0.001	45	Capsule area Number of capsules
Female volume—egg size	0.0003	0.996	269	Capsule area Number of capsules
Female volume—hatching size	−0.078	0.262	210	Capsule area
Capsule area—number of eggs per capsule	−0.1408	0.021	269	Female volume
Capsule area—number of embryos per capsule	0.608	< 0.0001	315	Female volume
Capsule area—number of hatchlings per capsule	0.2858	< 0.0001	210	Female volume
Capsule area—egg size	−0.0185	0.763	277	Female volume
Capsule area—hatching size	0.1067	0.124	210	Female volume Number of capsules
Number of capsules—hatching size	−0.245	0.725	210	Female volume Capsule area
Number of hatchling per capsule—hatching size	−0.1743	0.012	210	Female volume

(*) Pearson product–moment correlation

(**) Partial Pearson correlation using as controlling factor(s) the variables which showed a significant correlation and controlling by female volume

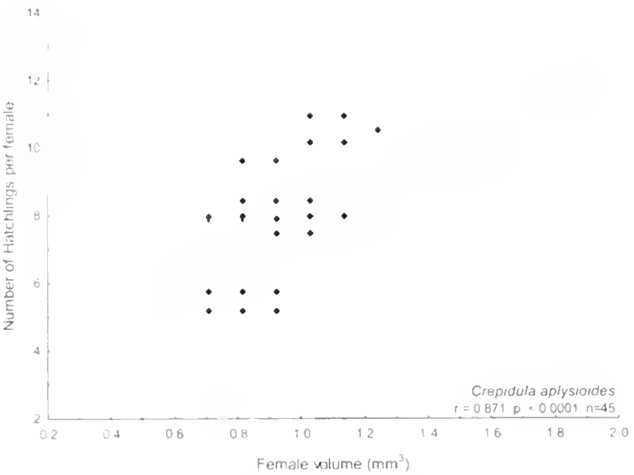


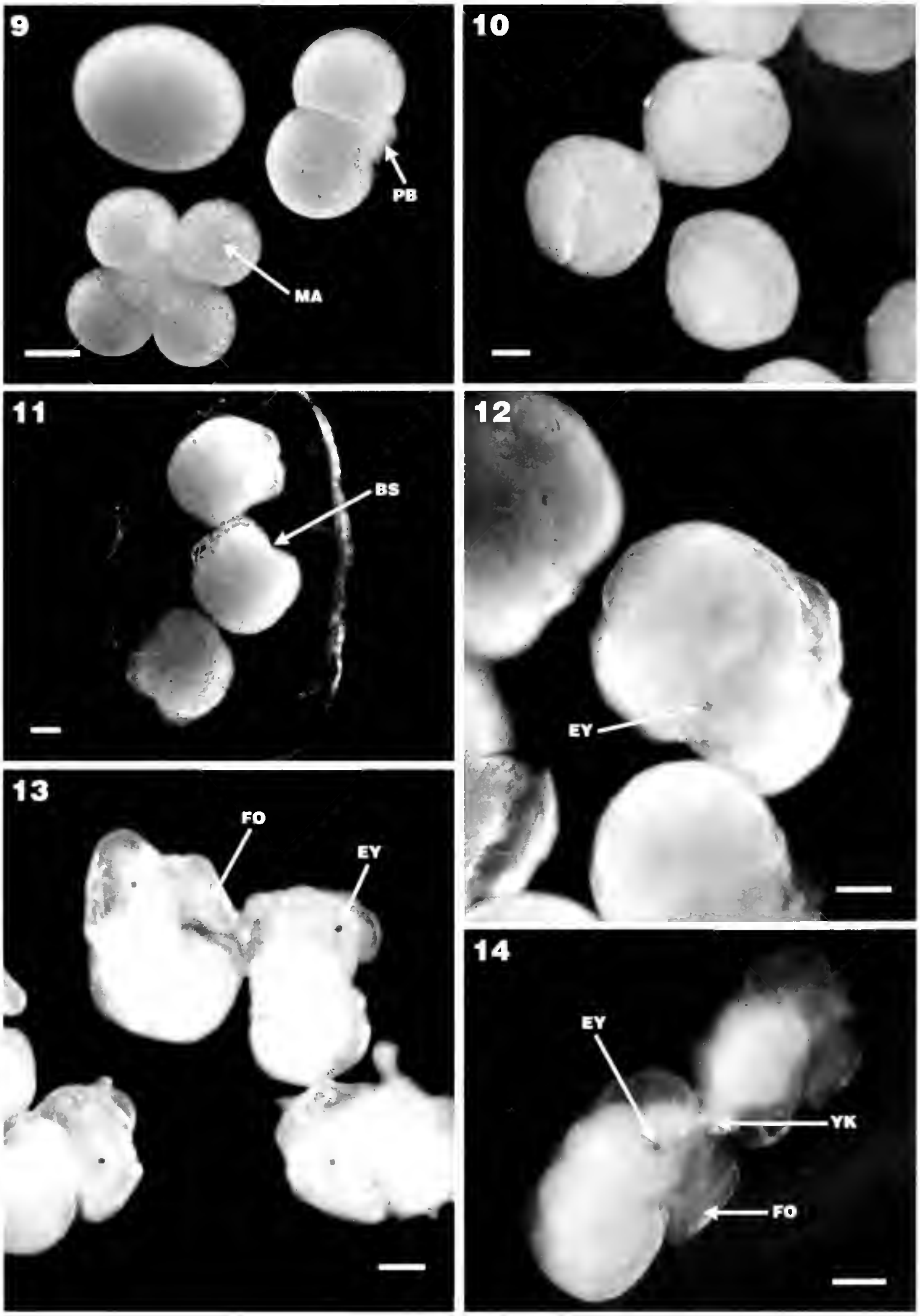
Figure 8. Relationship between female size (volume) and number of hatchlings per capsule of *Crepidula aplysioides*.

and overgrow the macromeres at the vegetal pole (Figure 10). The gastrula measured around 350 µm in diameter (Figure 11) and the trochophore (Figure 12) measured around 370 µm including the small velar lobes. The early veliger measured around 430 µm (Figure 13), it had eyes and a small velum. The veliger (II) stage measured around 460 µm (Figure 14), it was characterized by a round bilobed velum, small cephalic tentacles and the organic matrix of the shell. The foot develops and the intracapsular pediveliger stage (Figure 15) was characterized by a reduced velum, short and thick cephalic tentacles; the shell of this pediveliger measured around 560 µm and was starting to calcify. Prior to hatching, the soft body showed brown pigmentation and a calcified shell measuring around 590 µm in length (Figure 16). At hatching, the shell measured around 800 µm, the hatchling was characterized by a small round velum and a large foot (Figure 17). An interesting observation was the fact that the pediveligers hatched from the egg capsules but remained inside the brooding chamber of the mother for a few days, protected by its mantle cavity and shell (Figure 18). When the pediveligers crawled out of this brooding chamber, their shell had a minimum size of 1000 µm and the velum had resorbed completely (Tables 5 and 6). The number of hatchlings was significantly lower (by one individual) than the number of eggs (t-test, $p < 0.001$). This difference is attributable to cannibalism, which we observed among sibling embryos in a few egg capsules, usually larger embryos feeding on a smaller one.

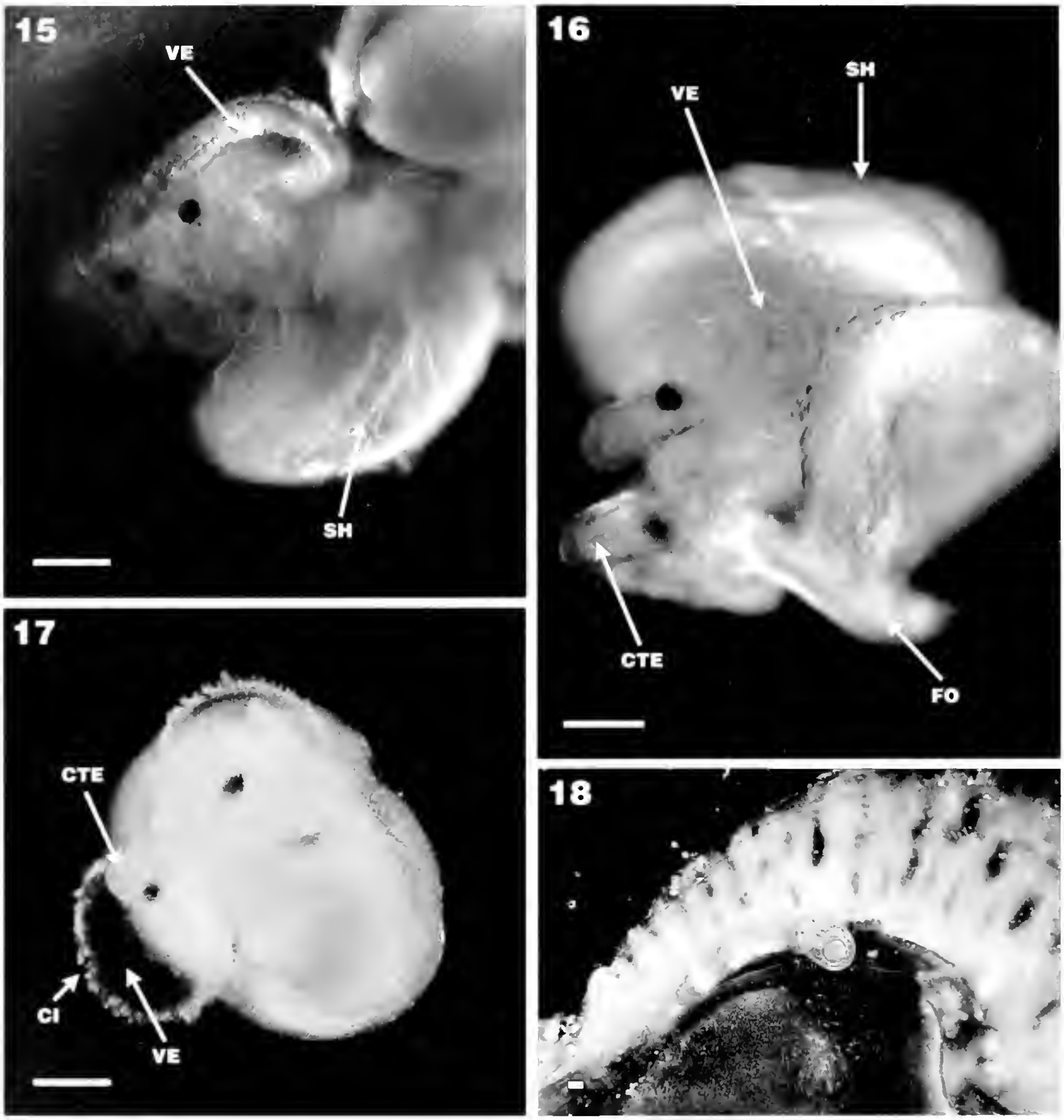
Crepidula aplysioides: Each female broods between 11 and 40 egg capsules (mean = 23.4 ± 4.5, n = 45, Figure 19). The egg capsules had a triangular shape, with one corner extending to form a stalk by which all the egg capsules were attached to the substrate at a common point. The capsule walls were thin and transparent. Egg capsules measured 0.5–2.4 mm length (excluding the stalk), 0.7–2.7 mm width and the thread-like stalk measured 0.6–3.3 mm length (Table 4). The number of eggs per capsule varied from 3 to 18. The uncleaved egg measured about 300 µm (Figure 20) and all eggs underwent normal cleavage and developed (Figures 21–24). Development was very similar to *C. navicula*: the gastrula measured around 350 µm diameter (Figure 25). The ciliated trochophore (Figure 26) was very active inside the egg capsule, rotating and moving constantly. These embryos were yellow, measured about 484 µm, and had the organic matrix of the shell and eyes. No significant differences were observed between the number of eggs and the number of embryos at this stage ($p = 0.1472$) and nurse eggs were not observed. During development, a small round velum develops (Figures 27–30). Hatching occurs as crawling pediveligers measuring about 600 µm in shell length (Figure 31). These pediveligers had the ability to swim very closely to the substrate and when in contact with any surface, they crawled. The number of hatchlings was significantly lower (by one individual) than the number of eggs (t-test, $p = 0.01597$). This difference would be due to cannibalism, a phenomenon we observed among sibling embryos in one egg capsule, in which one embryo suddenly lost all its yolk content to the egg capsule and the rest of the embryos started feeding on it immediately. The emptied embryo survived for a few days and then died (Figures 32, 33). We measured the embryonic shell of 12 adult individuals and found that it measured 590 ± 39 µm in length which did not differ significantly from the size of the shell at hatching

Table 4. Egg capsule dimensions of *Crepidula navicula* and *Crepidula aplysioides*. Values represent mean ± SD, numbers in parenthesis indicate range.

Species	Egg capsule shape	Width (A) mm	Length (B) mm	Stalk (C) mm
Crepidula aplysioides		1.44 ± 0.36 (0.65–2.73) n = 187	1.12 ± 0.26 (0.50–2.15) n = 187	1.44 ± 0.54 (0.60–3.32) n = 176
Crepidula navicula		1.2 ± 0.2 (0.8–1.6) n = 153	0.9 ± 0.1 (0.50–1.3) n = 153	1.0–1.2



Figures 9–14. Embryonic development of *Crepidula navicula*. **9.** Egg stage; one of the embryos is at the 4 cell stage. **10.** Gastrula. **11.** Trochophore. **12.** Early veliger (I). **13.** Veliger (II). **14.** Veliger (III).



Figures 15–18. Embryonic development of *Crepidula navicula*. **15.** Pediveliger. **16.** Prehatchling. **17.** Hatchling. **18.** Crawling juveniles hatching from the brooding chamber. Abbreviations: AP: animal pole, BS: blastopore, CTE: cephalic tentacles, EY: eye, FO: foot, MA: macromere, MI: micromere, MSH: matrix of shell, PB: polar body, PM: plasma membrane, SH: shell, VE: velum, VG: vegetal pole, YK: yolk. Scale bar = 100 µm.

($p = 0.968$) thus the absence of a planktotrophic stage is confirmed (Tables 5, 6).

DISCUSSION

Size at Sexual Maturity

In these protandric species, the overlap between male and female size is common (Collin, 1995). In nature, the transition from male to female may depend on the availability of a mate and of the relationship between body size and the reproductive demands of each sex. In this study, we observed the genital papilla in specimens of *C. aplysioides* larger than 7.5 mm in shell length. From the total number of females, only 62.5% of them were brooding egg capsules, this is comparable to results obtained by Collin (2000b) in two *Crepidula* species from the coast of San Juan Island, Washington State (Pacific coast of North America). The first is *Crepidula adunca* Sowerby, 1825, which broods throughout the year, with a maximum proportion of 66% brooding females between January and February, and the second is *Crepidula lingulata*, which reproduces in the summer with a

Table 5. *Crepidula navicula* and *Crepidula aplysioides*. Characteristics of embryos during intracapsular development. Values represent mean ± SD, numbers in parenthesis indicate range

Stage	Characteristics	*C. navicula* size of embryos (µm)	*C. aplysioides* size of embryos (µm)
Egg	Uncleaved yellow egg	329 ± 28 (293–360) n = 67	317 ± 59 (200–468) n = 277
Gastrula	Yellow embryos, round with flattened edge at the site of the velar lobes (not developed). Movement	349 ± 29 (320–400) n = 102	350 ± 19 (320–368) n = 7
Trochophore (preveliger embryo)	Development of small, ciliated velar lobes, rotates around itself	369 ± 32 (320–440) n = 50	352 ± 33 (300–400) n = 72
Veliger (I)	Eyes, growth of velum	434 ± 15 (400–440) n = 13 (velum 174 µm across)	No measures
Veliger (II)	Organic matrix of shell, velum, very small cephalic tentacles, the foot begins to differentiate	460 ± 41 (400–560) n = 36 (velum 368 µm across)	447 ± 19 (420–480) n = 7
Veliger (III)	Development of foot begins, non calcified shell, larger velum	446 ± 36 (400–520) n = 44 (velum 446 µm across) (foot 268 µm in length)	424 ± 22 (400–480) n = 21 (velum 523 µm across and each lobe measures 224 µm) (foot 245 µm in length)
Pedveliger	Calcification of shell, small foot and short cephalic tentacles, reduction of velum	561 ± 98 (440–720) n = 28	No measures
Prehatching	Bilobed and round velum, well developed foot, calcified yellow shell, purple-brown pigmentation of foot and mantle	590 ± 76 (480–760) n = 55	450 ± 38 (330–540) n = 51 (velum 484 µm across, each lobe measures 233 µm in diameter, each cilia measures 120 µm in length) (foot 288 µm in length)
Hatching	Similar to prehatching but larger and stronger shell. Operculum was not observed in any stage.	814 ± 140 (550–1172) n = 24 Shell with white spots (velum measures 800 µm across and 360 µm in lobe diameter)	619 ± 95 (400–850) n = 186 Shell with brown spots

Table 6. Summary of the reproductive characteristics of *Crepidula navicula* and *Crepidula aplysioides*. Values represent mean ± SD, numbers in parenthesis indicate range

Species	Number of capsules per female	Capsule length (mm)	Eggs per capsule	Hatchlings per capsule
Crepidula navicula	8.5 ± 2.2 (5–15) n = 40	0.92 ± 0.15 (0.52–0.13) n = 153	3.9 ± 1.0 (3–6) n = 18	2.8 ± 0.8 (1–4) n = 22
Crepidula aplysioides	23.4 ± 4.5 (11–40) n = 45	1.1 ± 0.3 (0.5–2.1) n = 187	7.6 ± 2.5 (3–18) n = 58	6.5 ± 2.1 (3–13) n = 48

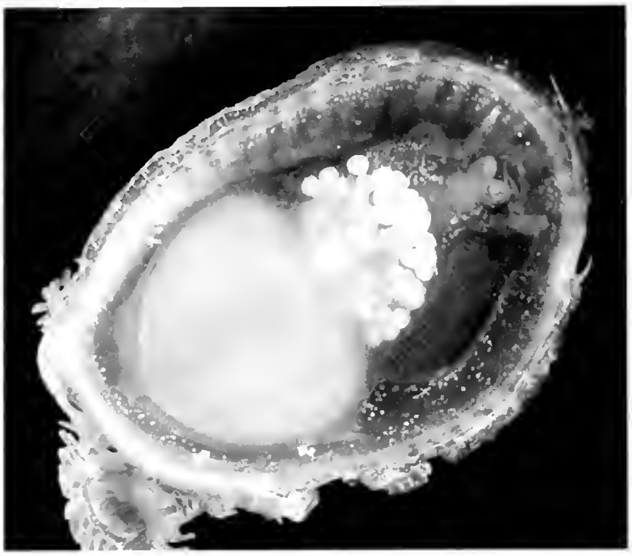


Figure 19. Ventral view of female of *Crepidula aplysioides* with brood.

maximum proportion of 61–62% brooding females between June and August.

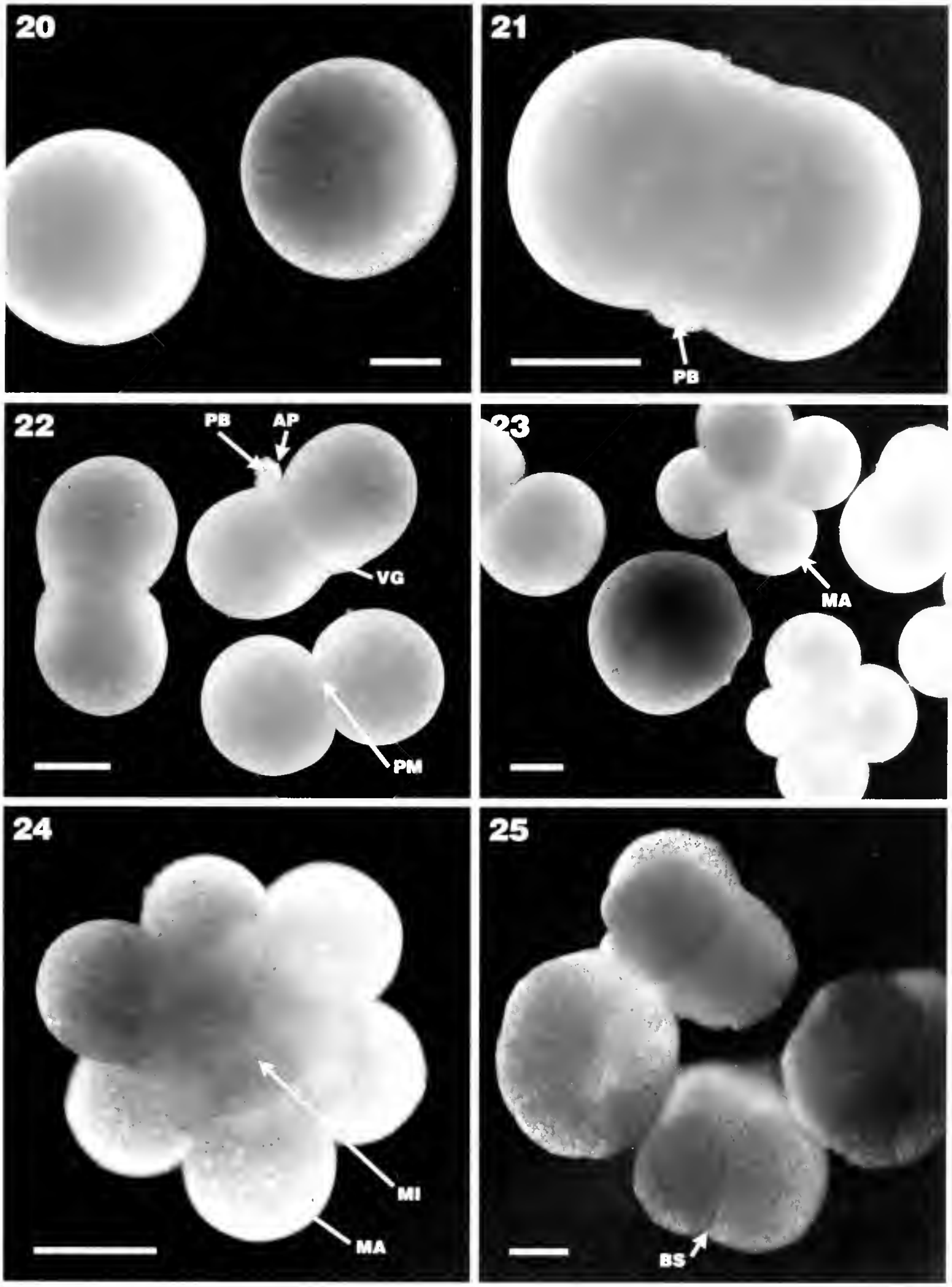
Female Shell Length and Spawn Relationships

A correlation between female size and egg capsules per brood is a common feature of calyptraeid species (e.g. Hoagland, 1986; Chaparro et al., 1999; Collin, 2000b); however, our results confirmed this hypothesis to be true only for *C. aplysioides*. Chaparro et al. (1999) reported that in *C. dilatata* Lamarck, 1822, egg capsule size (height and width), the weight of the capsule wall, and the number of eggs per capsule increased with shell length in females; however, the number of embryos per capsule, egg diameter, and number of capsules per brood were independent of female shell length. In this work we found that female size is an important parameter related to fecundity in *C. aplysioides*, since it is associated with number of eggs, number of embryos, and number of hatchlings. In *C. navicula*, the same parameter affects capsule size. What seems to be consistently important for both species is the fact that the number of eggs, embryos, and hatchlings contained in each capsule is dependent on capsule size, probably due to space limitations, so if capsule size is limited by female size as is the case of *C. navicula*, the final result is that smaller females are less fecund than larger ones in juvenile production. In the case of *C. aplysioides*, a difference in size of 5 mm in shell length (around 500 mm in volume) is very significant in terms of juvenile production. A small female produces few capsules with few hatchlings (around 75 hatchlings per female) while a large female produces many capsules with many hatchlings (more than 400 hatchlings). The term "female size" as used in this study involves not only shell length but also shell height and width; this is particularly necessary for *Crepidula* species since they grow on limited-size substrates such as the shell of other small gastropods. In the case of *C. navicula*, we observed small individuals attached to the gastropods *Tricolia tessellata* Potiez and Michaud, 1838, which is a very small species, and to *Cerithium eburneum* Bruguière, 1792, which has a very irregular surface. These two gastropods inhabit the sand under and around turtle grass, while the main host *M. modulus* is epifaunal on the blades of that seagrass. It is possible that some hatchlings fall from the host shell to the bottom where they would actively seek a host shell. Putnam (1964) reported the relationship between *C. adunca* Sowerby, 1825, and its host, the gastropod *Tegula funebralis* A. Adams, 1854. In this species, hatching occurs as crawling juveniles and less than 10% of the brood remain on the parental host, becoming quiescent sooner than those that fall off, which in turn are quite active.

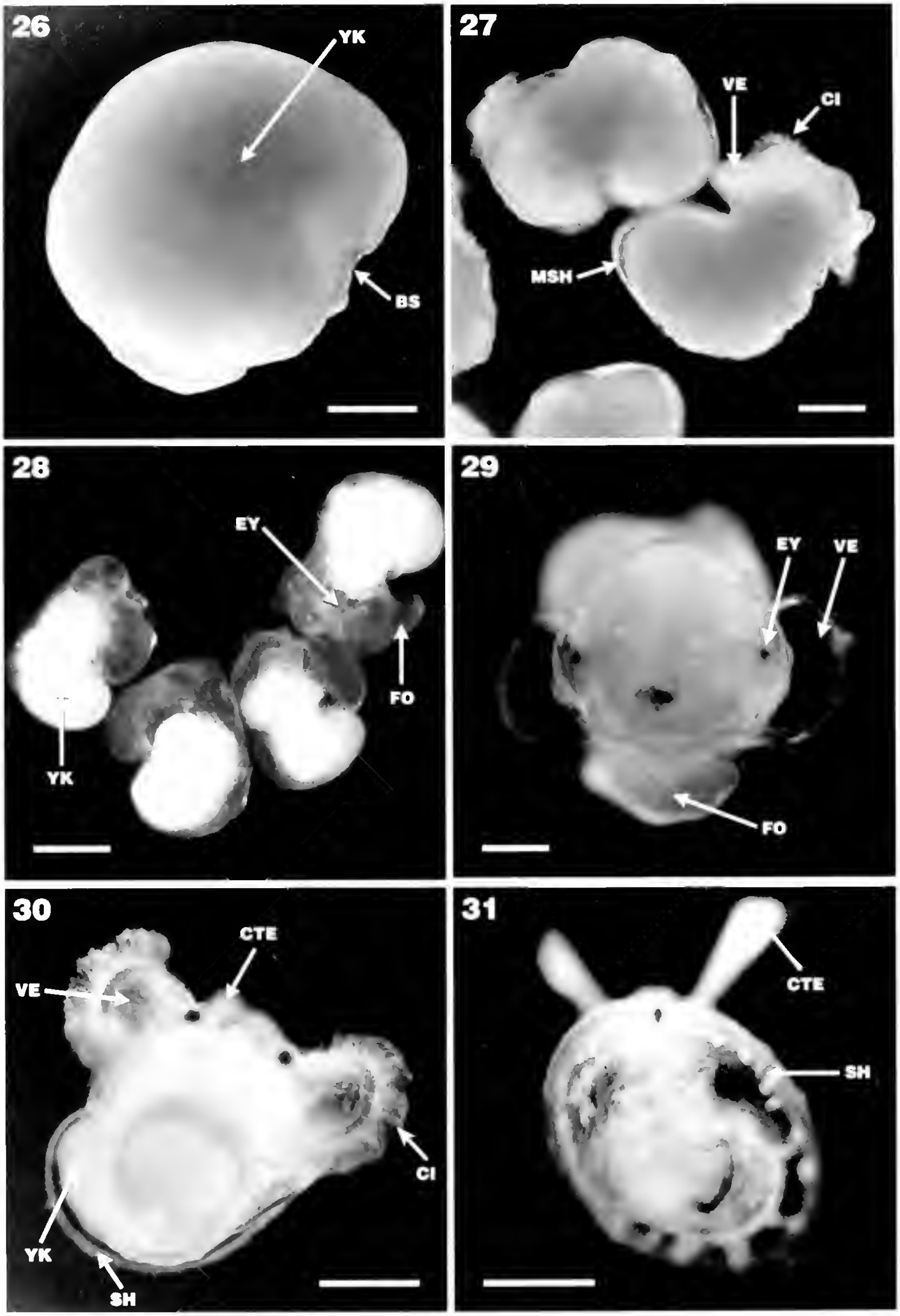
Development

Crepidula species are usually very productive with respect to the number of capsules brooded by each female. The lowest value reported by Hoagland (1986) was for *C. adunca* and *C. aculeata* that brood between 8–12 and 8–14 egg capsules respectively, while the highest value was for *C. fecunda* and *C. fornicata* that brood up to 75 egg capsules, a difference that is most likely due to species size. In terms of number of egg capsules brooded per female, we observed a significant trend within the genus *Crepidula*, for smaller species brooding less capsules than larger ones (Pearson correlation: $r = 0.510$, $p = 0.01$, $n = 22$, Figure 34). *Crepidula navicula* broods 5–15 egg capsules, which is lower than the previous report for *C. navicula* (10–20 egg capsules per brood). This value, however, is similar to the fecundity of *C. cf convexa* from Panama, which broods 7–16 capsules per female (Hoagland, 1986). In the present study, the two species are very similar both morphologically and regarding development. The females of *C. aplysioides* are larger and produce more egg capsules with more eggs than females of *C. navicula*, which, on the other hand, produce larger eggs and larger hatchlings. This coincides with the observations by Hoagland (1986) on calyptraeids: smaller species tend to have larger, fewer, yolkier eggs and fewer egg capsules than larger species.

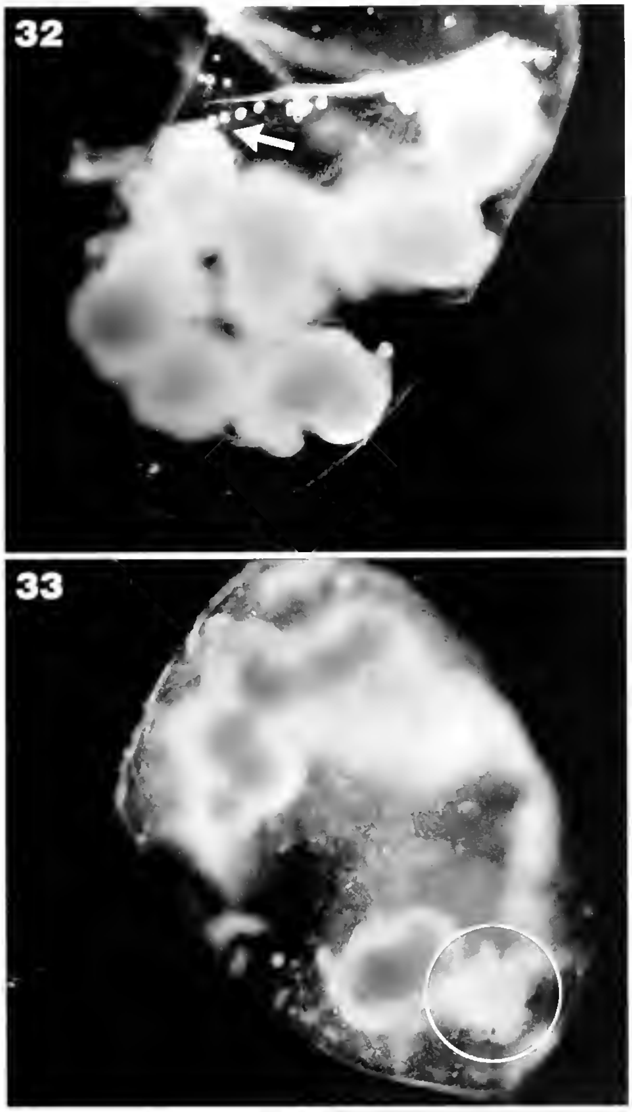
Development in both species was synchronous: all embryos within one brood were at the same stage of development and hatched at the same time. This is common among other calyptraeids, in several *Crepidula* species (Hoagland, 1986), and in *Crucibulum auricula* Gmelin, 1791 (Miloslavich and Penchaszadeh, 2001). However, Putnam (1964) reported that not all egg capsules under a given female of *C. adunca* are necessarily at the same stage of development or hatch at the same time. Adelphophagy or nurse egg ingestion has been reported in at least 7 *Crepidula* species and cannibalism of damaged or abnormal embryos is widespread in the genus (Hoagland, 1986). In our two *Crepidula* species,



Figures 20–25. Embryonic development of *Crepidula aplysioides*. **20.** Egg stage. **21.** First cleavage. **22.** First cleavage completed. **23.** Four cell stage. **24.** Abnormal cleavage. **25.** Gastrula.



Figures 26–31. Embryonic development of *Crepidula aplysioides*. **26.** Trochophore (arrow indicates blastopore). **27.** Early veliger I. **28.** Veliger II. **29.** Veliger III (foot is starting to develop). **30.** Pediveliger. **31.** Hatchling. Scale bar = 100 µm.



Figures 32–33. **32.** Egg capsule of *Crepidula aplysioides* showing droplets of yolk from an emptied embryo. **33.** The same egg capsule showing in a circle the empty embryo that survived only a few days, while the rest of the embryos fed on the yolk.

nurse eggs were not observed and cannibalism of one or two embryos was observed in few egg capsules. The egg and hatchling production of both species is very variable (Table 6). For *C. navicula*, the lowest egg production was 15 eggs per female and the highest 90 (average 33 eggs per female), while the lowest production of hatchlings was 10 per female and the higher was 60 (average 25 hatchlings per female). For *C. aplysioides*, the production per female is in average 5–6 times greater in comparison to *C. navicula*; in this species, the lowest egg production was 33 eggs per female and the highest 720 (average 166 eggs per female), while the lowest production of hatchlings was 33 per female and the higher was 520 (average 152 hatchlings per female).

The size of the uncleaved egg of *C. navicula* and *C. aplysioides* is within the size range of other *Crepidula* species, 150–420 µm (Hoagland, 1986). In these two species, egg size is particularly important because yolk would be almost the only food source available for the embryo during intracapsular development, given the absence of nurse eggs and limited cannibalism. Development of *C. navicula* and *C. aplysioides* is synchronous within and among egg capsules of a single female; however, they reach variable sizes (Table 5) probably depending on the yolk reserves of the egg (which also has variable sizes) (Table 5). Hoagland (1986) reported that for most calyptraeids, larvae develop synchronously, except for those with nurse eggs.

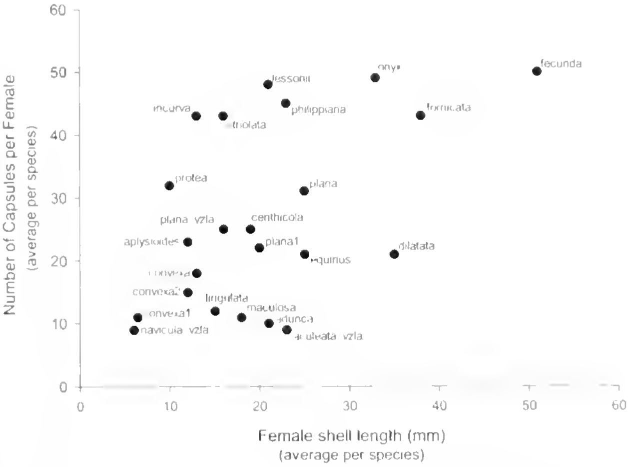


Figure 34. Relationship between female size (shell length) and number of capsules brooded per female reported in the species of the genus *Crepidula*. Sources: Gallardo, 1977; Hoagland, 1986; Collin, 2000b, Cledón and Penchaszadeh, 2001; Miloslavich et al. (In press). *Crepidula plana* (unpublished data) and present study.

About half of the *Crepidula* species reported by Hoagland (1986) hatch as free-swimming veligers and the other half hatch as crawling juveniles. Of these, most of the tropical Caribbean and Gulf of Mexico species have direct development and lack a free swimming stage: *C. aculeata*, *C. convexa*, *C. maculosa*, and *C. plana* from Florida (Hoagland, 1986) and *C. porcellana* Lamarck from tropical west Africa (Knudsen, 1950). *C. navicula* from the Bahamas also hatches as a crawling juvenile (Hoagland, 1986). In this paper, the two species hatch as crawling pediveligers with a very limited swimming capability and remain very close to the substrate. This reproductive pattern for tropical calyptraeids would be another exception to "Thorson's rule" (Thorson, 1946, 1950) that proposes that species with planktonic larvae are predominant in tropical marine environments (see review by Gallardo and Penchaszadeh, 2001).

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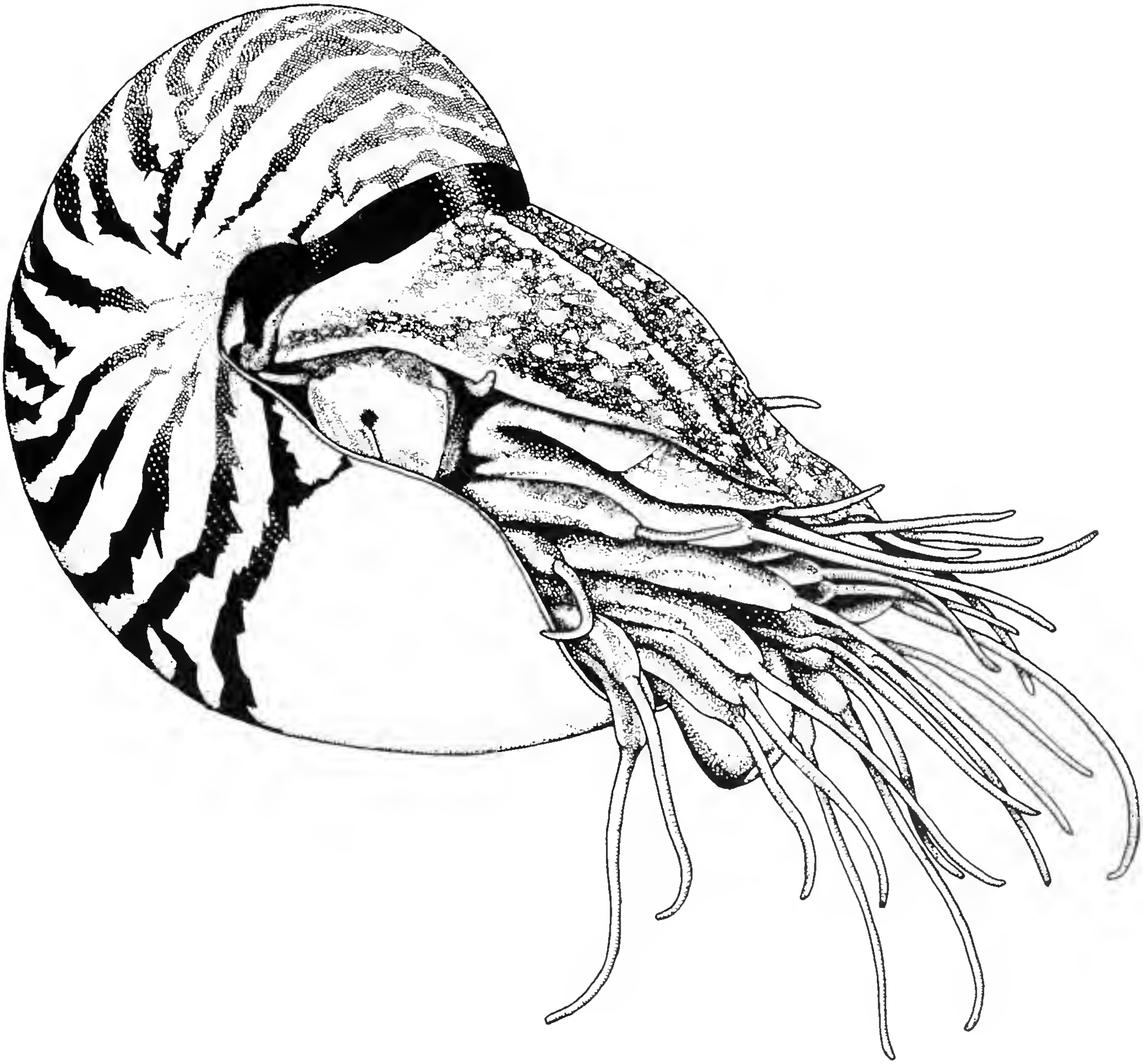
THE NAUTILUS

Volume 117
2003



AUTHOR INDEX

NEW TAXA PROPOSED IN VOLUME 117 (2003)

GASTROPODA

Amalda josecarlosi Pastorino, 2003, new species (Olividae) 16
Horaiclavus sysoevi Smriglio and Mariottini, 2003, new species (Drilliidae) 85
Macron vermeiji Nielsen and Frassinetti, 2003, new species (Pseudolividae) 91
Metula (Metula) miocenica Schmelz and Portell, 2003, new species (Colubrariidae) 12
Neolepton georgianum Zelaya and Ituarte, 2003, new species (Neoleptonidae) 8
Neolepton holmbergi Zelaya and Ituarte, 2003, new species (Neoleptonidae) 10
Pseudococculina rimula Simone and Magenta, 2003, new species (Pseudococculinidae) 70
Scabrotrophon inspiratum Houart, 2003, new species (Muricidae) 87
Triumphus mautenlalmensis Nielsen and Frassinetti, 2003, new species (Pseudolividae) 95

BIVALVIA

Bathymodiolus tangaroa von Cosel and Marshall, 2003, new species (Mytilidae) 31
Carditella galapagana Coan, 2003, new species (Condylocardiidae) 57
Carditella marieta Coan, 2003, new species (Condylocardiidae) 57
Condylocardia elongata Coan, 2003, new species (Condylocardiidae) 54
Condylocardia fernandina Coan, 2003, new species (Condylocardiidae) 53
Condylocardia geigeri Coan, 2003, new species (Condylocardiidae) 56
Condylocardia kaiserae Coan, 2003, new species (Condylocardiidae) 54
Condylocardia koolsae Coan, 2003, new species (Condylocardiidae) 53
Condylocardia sparsa Coan, 2003, new species (Condylocardiidae) 50
Gigantidas gladius von Cosel and Marshall, 2003, new species (Mytilidae) 38

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446

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